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TAXONOMIC AND BIOLOGICAL STUDIES OF NEOTROPICAL FIG WASPS (HYMENOPTERA: AGAONIDAE)

By

William Ramirez B.

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Taxonomic and Biological Studies of Neotropical Fig Wasps (Hymenoptera: Agaonidae)[1]

WILLIAM RAMÍREZ B.

ABSTRACT

Seven new species of New World *Blastophaga* which develop in the receptacles of figs of the subgenus *Urostigma,* section *Americana,* are described. The hosts of several previously described agaonids have been found or corrected. *Urostigma* species were found to be always pollinated by *Blastophaga* and *Pharmacosycea* species by *Tetrapus,* as was supposed by Müller in 1887 but contrary to views of certain recent authors.

Blastophaga wasps of the New World are all placed in the subgenus *Pegoscapus* and are characterized by the presence of corbiculae on the front coxae (except *B. mariae* and *B. carlosi*) and the mesosternum. These structures are used to carry pollen; little or none is carried in the gut or on the body surfaces. *Tetrapus* females do not possess corbiculae but much pollen was found in the digestive tracts and on the body surfaces of specimens examined.

The sizes of the bodies and ovipositors of the species of *Blastophaga* studied were different. Larger *Blastophaga* usually develop in species of *Ficus* which possess larger receptacles.

Since their wasps are quite host specific, *Ficus isophlebia, F. jimenezii,* and *F. tuerckhemii* are three well defined biological species as described by Standley in 1917, and not just one species *(F. tuerckheimii). F. hemsleyana* and *F. turbinata* are also well defined species, each with its own pollinator, and not one species *(F. citrifolia).* Each of the pharmacosyceous *F. crassiuscula* and *F. glabrata* has its own pollinator (*Tetrapus costaricanus* and an undescribed *Tetrapus* respectively), and thus should not be considered as one species *(F. insipida).* These conclusions concerning fig species are contrary to the recent views of DeWolf.

INTRODUCTION

The purposes of the present work are to clarify the generic status of New World Agaonidae, to describe seven species of *Blastophaga* which have been

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collected from New World figs (*Ficus*), subgenus *Urostigma*, section *Americana*, to present comparative and host data on other species together with some comments on fig species, to provide a key to Costa Rican Agaonidae, and to summarize biological information on New World Agaonidae.

It is well known that species of *Ficus* are absolutely dependent for pollination upon small wasps of the family Agaonidae, but there are arguments about the specificity of these pollinators. Van der Pijl (1960) indicated surprise that the genus *Ficus*, each species with its own gall wasp pollinator, still flourishes. Baker (1961) did not accept the specificity of fig wasps; however, in a later publication (Baker and Hurd, 1968) he changed his view and points out that in the enormous genus *Ficus* a unique situation prevails in which almost every species of fig has a recognizably different chalcidoid pollinator.

At present there is strong evidence that agaonid wasps are very specific to their hosts. It is also known that different genera and subgenera are quite specific to the different groups of figs (Wiebes, 1963; Hill, 1967a).

In the New World there are two subgenera of *Ficus*, *Urostigma* and *Pharmacosycea*. *Urostigma* is represented by section *Americana*, and *Pharmacosycea* by section *Pharmacosycea* (Corner, 1958).

Pharmacosycea and *Urostigma* in the New World are pollinated by different genera of agaonids, *Tetrapus* and *Blastophaga* respectively; there are no other New World agaonids. Müller (1887) correctly stated that *Tetrapus* appears to be limited to *Pharmacosycea*. Wiebes (1963) also reported that *Tetrapus* wasps develop in *Pharmacosycea* (section *Pharmacosycea*). Hill (1967a,b), however, considered that *Tristaniella* and *Secundeisenia* (=*Blastophaga*) also develop in section *Pharmacosycea*, an error resulting from misidentification of figs by earlier workers.

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Special thanks are due to my wife, Carmen L. de Ramírez, for her patience and endurance helping in the typing o the manuscript, and to Mrs. Joetta Weaver for typing the definitive copy.

MATERIALS AND METHODS

Sources of the agaonids: The material was collected mostly by the author in Costa Rica from 1964 to 1967. Some figs and wasps, however, were collected in Venezuela, Panamá and San Andrés Island, Colombia, during the years 1966 and 1967.

The places and dates of collection are given in Table 1. The country is omitted for Costa Rican localities.

The species of *Ficus* studied were: *F. colubrinae* Standl., *F. coombsii* Warb., *F. costaricana* (Liebm.) Miq., *F. crassiuscula* Warb., *F. glabrata* H.B.K., *F. hemsleyana* Standl., *F. isophlebia* Standl., *F. jimenezii* Standl., *F. lapathifolia* (Liebm.) Miq., *F. nymphaeaefolia* P. Mill., *F. obtusifolia* H.B.K., *F. oerstediana* Miq., *F. schippii* Standl., *F. torresiana* Standl., *F. trachelosyce* Dugand, *F. tuerckheimii* Standl., *F. turbinata* Pitt., *F. velutina* Willd. and *Ficus* No. 4.* *F. aurea* Nutt., *F. myriacycea* Pitt. and *F. radula* H. and B. were studied in less detail.

Floral cycle of figs: Galil and Eisikowitch (1968) divide the developmental phases of a syconium in a useful way which I have followed, thus:

Phase A (Pre-female): young syconium prior to the opening of the ostiole.

Phase B (Female): ostiolar scales loosen, female flowers ripen, sycophilous wasps penetrate into the syconium and oviposit into the ovaries.

Phase C (Interfloral): wasp larvae and fig embryos develop within their respective ovaries. Ovaries occupied by the larvae are transformed into galls.

Phase D (Male): male flowers mature, wasp reach the imago stage, fertilized female wasps leave the syconia via channels bored by the males.

Phase E (Post-floral): both the syconia and the seeds inside them ripen.

Measurements of wasp structures were made with an eyepiece micrometer at 430 × for mandibles and for the mesosomal dorsum of the male, 30 × for body length and ovipositor length. Ten specimens were measured in all cases except for *Blastophaga ileanae,* for which only five were available. Measurements given are means, except for ranges shown for mandibles in Table 2.

Collecting of fig wasps and figs: Individual syconia which were starting to ripen were collected from each species of *Ficus.* The best fruits were those starting to change color and to soften. Each fig was opened into halves and placed in a small jar that contained on the bottom some dry toilet paper in order to absorb moisture from the fig. Once all the wasps emerged from their galls, usually one day after the opening of the figs, a small section of toilet paper wet with gasoline was put inside the jar to kill the wasps. Once

* *Ficus* No. 4 is very common in Estado Sucre, Venezuela. It is characterized by the presence of sessile and geminate figs, which are green when ripe and measure about 2 cm in diameter. The leaves are glabrous, basally cordate, and apically obtuse. A specimen is deposited at the University of Costa Rica, Department of Biology Herbarium, as *Ficus* No. 4, Venezuela, collector William Ramírez.

TABLE 1. *Fiscus* Species and Localities Involved in this Study.

	Vial No.	Place	Date
Subgenus *Urostigma*			
F. colubrinae	13	Puerto Viejo, Heredia	May 16, 64
F. coombsi	438	San Andrés Island, Colombia	Aug. 5, 67
F. costaricana	27	La Luisa, Sarchí, Grecia, Alajuela	Apr. 16, 64
F. hemsleyana	44	Sarchí, Alajuela	July 17, 64
	45	Santo Domingo, Heredia	July 19, 64
	46	Hatillo No. 2, San José	July 21, 64
	432	Munegro, Cumaná, Sucre, Venezuela	July 15, 66
F. isophlebia	48	Ciruelas, Alajuela	Aug. 20, 64
	196	Camino Playas del Coco, Guanacaste	June 2, 67
F. jimenezii	51	Alajuela	Apr. 1, 64
	53	San Pedro de Poás, Alajuela	Apr. 1, 64
	54	Uriche, Heredia	Apr. 10, 64
	55	Santo Domingo, Heredia	Apr. 19, 64
	59	Barba, Heredia	May 6, 64
	60	Barba, Heredia	June 3, 64
	219	Paraíso, Cartago	Dec. 20, 66
	220	Arenal, Tilarán, Guanacaste	July 15, 65
	221	Arenal, Tilarán, Guanacaste	July 15, 67
F. lapathifolia	66	Grecia, Alajuela	May 25, 64
	191	Hatillo No. 2, San José	June 14, 64
F. nymphaeaefolia	176	Puerto Viejo, Heredia	May 16, 64
F. obtusifolia	172	Playón de Aguirre, Puntarenas	June 27, 64
	210	Grecia, Alajuela	Aug. 3, 64
	212	Tilarán, Guanacaste	July 14, 67
	213	Arenal, Tilarán, Guanacaste	July 14, 67
	215	Camino Cañas, Tilarán, Guanacaste	July 15, 67
	433	Ancon Hill, Canal Zone, Panamá	1967
	434	Barro Colorado Island, Canal Zone, Panamá	1967
F. oerstediana	88	La Virgen, Heredia	May 31, 64
F. schippii	169	Puerto Viejo, Heredia	May 16, 64
F. torresiana	4	Pejibaye, Turrialba, Cartago	July 29, 64
F. trachelosyce	174	Playón Aguirre, Puntarenas	July 2, 64
	230	Arenal, Guanacaste	July 14, 67
F. tuerckheimii	144	Potrero Cerrado, Cartago	Jan. 11, 64
	147	Poasito, Alajuela	May 6, 64
	149	San Jerónimo, Moravia, San José	May 1, 64
	154	Poasito, Alajuela	May 13, 64
	157	Los Angeles San Rafael, Heredia	May 23, 64
	158	El Roble, Heredia	May 31, 64
	159	San Jerónimo, Moravia, San José	May 1, 64
	160	Cot, Cartago	Mar. 12, 64
	161	Vista de Mar, Coronado, San José	Apr. 22, 64
	162	San Rafael, Heredia	Apr. 23, 64
	163	El Roble, Heredia	June 1, 64
	166	San Rafael, Heredia	June 23, 64
	217	Parque Central, San José	June 8, 67

	Vial No.	Place	Date
F. tuerckheimii x *F. jimenezii*	185	El Roble, Heredia	June 2, 64
F. turbinata	435	Santa Rosa, Sucre, Venezuela	June 2, 66
	436	Cumaná, Sucre, Venezuela	July 15, 66
	437	Panamá Viejo, Panamá	Mar. 18, 67
F. velutina	177	La Cañada, Cot, Cartago	Jan. 31, 63
	241	Paraíso, Cartago	Dec. 19, 66
Ficus No. 4	431	Cumaná, Sucre, Venezuela	June 27, 66
Subgenus *Pharmacosycea*			
F. crassiuscula	256	Vara Blanca, Heredia	July 16, 64
	257	San Vito de Java, Puntarenas	Mar. 24, 67
	258	San Vito de Java, Puntarenas	Mar. 24, 67
	260	La Carpintera, La Unión, Cartago	June 12, 67
	262	La Carpintera, La Unión, Cartago	June 12, 67
	263	Vara Blanca, Heredia	June 8, 67
	264	Canaán, Cerro Chirripó, Cartago	June 26, 67
F. glabrata	276	Puerto Viejo, Heredia	May 16, 64
	285	San Antonio de Belén, Heredia	Aug. 24, 64
	295	Río Guacimal, Guanacaste	Dec. 29, 66
	296	Miraflores, Canal Zone, Panamá	Dec. 12, 67

dead, they were brushed from the jar and the fruits. The agaonids were separated from their parasites and each species and its parasites was kept in a separate vial of 70% alcohol.

At the same time that wasps were collected, botanical material was obtained, pressed and dried for identification. The species of figs were identified using the papers by Standley (1917) and DeWolf (1960), and vouchers were deposited in the University of Costa Rica, Department of Biology Herbarium.

Dissection and mounting of the wasps: Each wasp was dissected in a depression slide in 70% alcohol before KOH treatment. Small hooks made of *minuten nadeln* mounted in sticks of wood were used as tools. After dissection, the wings were mounted and the other parts were put in small containers with 10% KOH for a period of about 12 hours at room temperature and then transferred to 70% alcohol for several hours. Hoyer's fluid was used to mount all the structures on slides, and proved to be superior for the wings and antennae; other media tried contract these structures and cause them to fold over or collapse.

The parts dissected and mounted from each female wasp were: head, antennae, mandibles, maxillo-labial complex, legs, wings, dorsum of thorax and abdomen, mesosternum, venter of abdomen and ovipositor. For males the structures dissected were: head, antennae, mandibles, legs, mesosomal dorsum (fused pronotum, mesonotum, metanotum, and propodeum), and abdomen. Once the slides were dry, the structures were projected for draw-

ing using a vertical micro-projector to facilitate outlining the structures. This type of projector proved to be best because the slides were horizontal at the time of projection and parts did not move. A phase microscope was used for details of the drawings.

Agaonid wasps from each species of *Ficus* from all localities and dates were dissected and identified in order to establish their specificity to the hosts.

In the descriptions, the number of sensilla per antennomere in the case of the female means the number of sensilla seen in dorsal aspect. In the case of male wasps, for the purpose of convenience, the prothoracic notum plus the fused mesonotum, metanotum, and propodeum are called "mesosomal dorsum." Unless otherwise stated the drawings were made in dorsal view.

The measurements are averages based on 10 specimens of each species, except as indicated in the footnote to Table 4.

BIOLOGICAL ACCOUNT OF NEW WORLD AGAONIDAE

In the New World figs the female flowers ("gall flowers" and reproductive female flowers) are intermixed with the male flowers and are scattered over all of the internal surface of the receptacle. The whole is termed a syconium or "fig fruit."

Agaonid females, after emerging from the ripe figs where they develop, search for a fig tree which possesses young figs at the right stage for pollination. Possibly the wasps are attracted by substances produced by the leaves and young receptacles. I have observed that for *B. cumanensis,* the pollinator of *Ficus* No. 4, several wasps were apparently attracted by the leaves, the wasps hovering near their edges. The possibility also exists that the syconium produces some kind of attractive substance when ready for pollination. In *Ficus* No. 4 the young syconia produce small drops of a translucent substance which accumulate on the exterior surface. This material did not have any detectable odor or flavor, but the receptacles which were in the right stage for pollination were very aromatic inside.

After the syconia buds appear, they remain small for a long period, then suddenly on any one tree all start growing almost simultaneously. Each species has a well defined period of development (pre-female phase) from the time that the syconia buds start growing to the time of penetration by the pollinators. This period is of course subject to weather conditions. I have found after several observations that for *Ficus* No. 4 this period is about 21 days.

When an agaonid lands on a young fig which contains female flowers in the receptive stage (female phase), she immediately moves about as though searching for the ostiole (the opening into the syconium). If it is a *Urostigma,* the *Blastophaga* locates the narrow slit below the most superficial ostiolar scale, raises the scale with the apical process of the first flagellomere,

and introduces the anterior part of the head in the opening, using the legs for pushing. Once the wasp has introduced the head, she uses the mandibles as a hold-fast while crawling between the scales. Each mandible possesses a proximal appendage which is armed with transverse ventral lamellae. The mandibles move alternately; the movements are so strong that the dorsal side of the head invaginates as a result of the contraction of muscles. The mandibular appendages and ridges prevent the wasp from moving back, permitting it only to move forward. About 15 minutes after it disappears under the most external ostiolar scale, her head appears at the internal opening of the ostiole. The wasp becomes completely free in the fig cavity in another 15 minutes. Contrary to the statements of Williams (1928), the abdomen is not particularly compressed in New World species and no liquid is squeezed out of it as the wasp enters the fig.

The ostiolar scales of the figs in subgenus *Urostigma* are located in such a way that the tunnel is first a helicoidal passage. Deeper in the ostiole the scales project inward, forming a straight channel. Thus a wasp entering the fig has to turn several times before she finds the straight portion of the ostiole. In her efforts at the time of entrance every wasp loses the wings and almost invariably also the last six flagellomeres. These parts are always left beneath the first, second, or third superficial ostiolar scales.

In *Pharmacosycea* figs, on the contrary, the ostiolar channel is a long tube which extends from the external ostiolar opening to the interior of the young fig. This channel is surrounded by scales all projecting toward the center; thus in *Pharmacosycea* the ostioles do not possess imbricated scales. Therefore the entering *Tetrapus* do not have to turn as *Blastophaga* do. *Tetrapus* wasps always reach the interior of the figs with complete antennae and wings.

An agaonid arriving at a tree with syconia in the right condition to be pollinated (female phase) seems to prefer a waspless one (apparently the wasp can distinguish whether a fig has been entered or not), but if more wasps arrive than the number of syconia present in the trees, then several wasps may penetrate the same fig. In 88 figs from a single tree (*Ficus* No. 4) I have found an average of 2 laying wasps per syconium (maximum 4, minimum 1).

In most New World species of *Ficus* almost every syconium of a tree is pollinated the same day, but in some pollination is over a period up to three days. If the young figs are not pollinated during this receptive period, even if wasps enter later, they stop growing, shrink and drop from the tree.

Once a *Blastophaga* is free inside of the fig, she walks around for several minutes. Using the remaining portions of the antennae, she searches the internal cavity and introduces the anterior part of her body among the stigmas, supposedly pollinating. In some cases the wasp spends more than an hour in this procedure. During this time she never uses the ovipositor, which is

located in the normal position and is directed posteriorly. After pollination the wasps start oviposition.

Probably the *Blastophaga* first pollinate all the female flowers (short- and long-styled) and next lay the eggs in the short-styled ones. The latter become gall flowers. The long-styled flowers are left presumably eggless due to the inability of the ovipositor to reach the ovary through the style.

The idea of pollination of all the flowers of the syconium (in male phase) prior to egg laying is supported by the finding of a single ripe syconium *(F. obtusifolia)* in Guanacaste, Costa Rica, which had only seeds, no galls. This syconium contained the remains of only one wasp, which I presume laid no eggs, so that all the flowers, short- and long-styled, developed into seeds.

Lerclerc du Sablon (1908) thought that flowers of caprifigs (=gall figs of *F. carica* L.) normally are pollinated and fertilized but that the development of their embryos is stopped by the growing wasp larvae. This idea was based on the observation that fertile achenes are frequently found among the gall flowers in mature caprifigs (Condit, 1932).

New World *Blastophaga* which are laying eggs are very aggressive towards each other, and if touched with a brush they bite the hairs and refuse to release them. Once several wasps have penetrated a single receptacle, a drop of latex plugs the ostiole; this latex is probably exuded from the lacerations produced on the ostiolar scales by the mandibles of the penetrating wasps.

In one tree of *F. turbinata*, wasps had entered a few figs on May 15, six days after the fruit buds started to grow. On May 16 at 7:00 a.m. 50% of the figs had wasps laying eggs; on May 17 at 3:00 p.m. eggs were being laid in all of the figs. The wasps were still laying eggs on May 18 at 8:30 p.m.; they remained very aggressive and their abdomens were compressed laterally. On May 19 at 3:30 p.m. the wasps were still alive but they were very quiet and egg laying had ceased. By this time the stigmas had wilted and the internal surfaces of the figs looked amber colored instead of white as they were at the time the wasps entered. On May 20 at 7:00 a.m. a few wasps were still alive but motionless. The new generation of wasps emerged from the ripe syconia about 30 days after their mothers entered the figs.

Wasps that have entered a fig never get out. Occasionally some apparently attempt to do so but die among the scales of the ostiole.

The period of development for each species of agaonid is apparently quite constant, being correlated with the ripening of the fig. I have recorded the period of development for the following species: *Blastophaga cumanensis*, 41 to 43 days in *Ficus* No. 4; *B. tonduzi*, 30 days in *F. hemsleyana; Blastophaga* sp. in *F. myriacycea*, 23 to 28 days; *B. baschierii* in *F. turbinata*, 26 to 30 days; and for the pollinator of *F. radula*, 27 days. At the end of the inter-

floral phase, almost all the syconia of a particular tree simulatneously increase rapidly in size and begin to soften. Once their volume is large enough in New World *Urostigma* figs a cavity is formed among the flowers inside the receptacle. In *Urostigma* the syconia usually start changing color at this period of development. As the figs begin to soften, the wasps become adults and the male flowers mature.

The first to emerge from the galls are the males which usually comprise less than 15% of the agaonid population of a fig. Each male makes a hole on the top of its gall to get out. Once out but still inside the syconium, a male finds a gall which contains a female of his own species, bites a hole in the top of the gall, introduces the telescoped abdomen through the opening and copulates with the female. The males are apterous and polygamous; each copulates with a number of females until no more virgins remain. After copulation (contrary to the observations of Grandi, 1961, for *B. psenes*) some males burrow out of the fig, usually through the ostiolar scales (in *Pharmacosycea* figs they always tunnel through the ostiolum) but in some *Urostigma* species they tunnel through any part of the fig wall. Several males usually make a tunnel simultaneously. Once they finish it, many of them drop to the ground. I have counted 2000 live males of *B. aguilari* per m^2 beneath a tree of *F. lapathifolia* from which wasps were emerging. If the males do not complete the tunnel, neither the female agaonids nor parasites can escape from the ripe figs.

The female wasps usually do not emerge from their galls until the exit tunnel has been completed. Then they emerge immediately. In the case of *Blastophaga* females, before they leave the syconium they go to the male flowers which are usually hidden under the galls and do not project into the internal cavity of the fig as far as the galls do. Each anther has two small slits which the wasps open with the antennal scapes and mandibles; through these openings the wasps remove the pollen from the anther sacks using the mandibles, front legs and possibly the antennae. They fill the four corbiculae (coxal and sternal corbiculae of Ramírez, 1969), and then go to the exits made by the males. Upon reaching the external surface of the fig, they clean the wings and abdomens using the hind legs, their heads are cleaned with the front legs. Next they fly to a fig tree of the same species in which they developed which possesses syconia at the right stage for pollination; they enter the figs, pollinate them and lay their eggs, thus initiating a new cycle.

In New World *Urostigma* there is usually no natural shedding of pollen with the exception of *F. tuerckheimii* in Costa Rica which is always pollinated and inhabited by two species of *Blastophaga* (*B. carlosi* and *B. mariae*). These two species are the only *Blastophaga* I have found in the New World which do not possess coxal corbiculae, and whose sternal corbiculae are very small in comparison to the *Blastophaga* inhabiting other species of *Urostigma*.

In *F. tuerckheimii* the anthers dehisce, shed the pollen, and the wasps become dusted with it at the time of their emergence from the galls.

After the normal emergence of the wasps from a *Urostigma* fig, almost all the anthers are wide open and empty. Every *Blastophaga* I have examined after emergence from its fig had the corbiculae full of pollen. However, wasps which had entered and died inside young figs after oviposition as a rule had the corbiculae empty or containing only a few grains of pollen.

In *Pharmacosycea* figs the anthers in the ripe figs are located more centrally than the gall flowers, and there is no true cavity. The anthers dehisce and shed the pollen, apparently without the help of the wasps. Thus the *Tetrapus* wasps which emerge from the galls inside the fig come in contact with the shed pollen and become completely dusted with it. To escape from the figs the females find the one exit which is made by the males through the ostiolum. The females apparently pollinate the young receptacles accidentally. Pollen was also found in the digestive tract of *T. costaricanus.*

In any particular area fig trees of the same species may be found with syconia in all phases of development (each tree with all syconia in the same stage of development). Thus it is possible for emerging females to find another tree of the same species with figs in the right stage for pollination. In this way fertilization is accomplished with pollen from a different tree.

The wasps always emerge at least one day before the fig is completely ripe. This mechanism saves the wasps from being eaten by birds, bats, and other animals that use the figs as a food.

SYSTEMATIC TREATMENT

New World Genera

The genus *Tetrapus* Mayr (1885) is adequately characterized by Grandi (1925) and the described Costa Rican species is keyed out below. The grouping of the American species of *Blastophaga,* however, requires discussion. At present there are thirty-four known species of New World *Blastophaga.* They were placed by Grandi (1963a) in five subgenera: *Julianella* (six species); *Tristaniella* (one species); *Valentinella* (seventeen species); *Secundeisenia* (two species); and *Pegoscapus* (one species). Seven others were placed by Grandi (1963a) in a special section because their wing venation was not known.

Grandi (1919, 1963b) used the venation of the front wing of the female as a main descriminatory character to distinguish *Julianella, Tristaniella,* and *Valentinella. Tristaniella* has complete humeral, marginal, stigmal, and postmarginal veins; *Valentinella* lacks the postmarginal vein (as in *Tristaniella* the costal cell is closed); and *Julianella* has an atrophied humeral vein, not reaching the edge of the wing, and the other veins are absent, the

costal cell open. Females of the other two subgenera, *Secundeisenia* and *Pegoscapus,* have front wing venation similar to that of *Valentinella;* these groups were recognized by Grandi largely for historical reasons.

The venational characters used by Grandi are variable and not correlated with other characters among the recognized subgenera. These subgenera, therefore, are not useful nor recognizable on any complex of characters. All new World *Blastophaga* should be placed under the subgeneric name *Pegoscapus,* as indicated in the following synonymy:

Subgenus **Pegoscapus** Cameron

Eisenia Ashmead, 1904, Mem. Carnegie Mus., 1(4):233. Type: *E. mexicana* Ashmead, 1904, by original designation. Not *Eisenia* Malm, 1877.

Pegoscapus Cameron, June 1, 1906, Primer Informe Anual de la Estación Central Agronómica de Cuba (1 Apr. 1904-30 June 1905), p. 275. Type: *P. longiceps* Cameron, 1906, by original designation.

Eiseniella Ashmead, July 13, 1906, Proc. Washington Entomol. Soc., 8:30. New name for *Eisenia* Ashmead. Not *Eiseniella* Michaelsen, 1900. For date of publication see Waterston, 1920.

Secundeisenia Schulz, 1906, Spolia Hymenopterologica, p. 146. New name for *Eisenia* Ashmead. (Schulz, on p. 356, cites *Eiseniella,* showing that *Secundeisenia* postdates *Eiseniella.*)

Allopade Strand, 1911, Arch. Naturgesch. (Berlin), 77(1):210. New name for *Eisenia* Ashmead.

Valentinella Grandi, 1919, Boll. Lab. Zool. Portici, 13:25. Type: *Blastophaga estherae* Grandi, 1919, designated by Gahan and Fagan, 1923, Bull. U.S. Nat. Mus., 124:1-173.

Julianella Grandi, 1919, Boll. Lab. Zool. Portici, 13:20. Type: *Blastophaga aguilari* Grandi, 1919, monobasic.

Tristaniella Grandi, 1936b, Boll. Ist. Entomol. Univ. Bologna, 26:239. Type: *Blastophaga astoma* Grandi, 1919, monobasic.

Female: Mandible with laminar process (appendage) with a variable number of transverse ridges (lamellae). Antenna with eleven free segments, pedicel in some species supplied dorsally with a very prominent subelliptical formation which occupies more than half of the segmental length. First flagellomere (third antennal segment) divided into two sections, a small proximal one and a distal scale-like elongate section. Second flagellomere subconical and usually without sensilla. Last seven flagellomeres with elongate sensilla and a variable number of bristles (some species possess also flattened bristles); last flagellomere with variable number of circular and elongate sensilla. Compound eye with minute hairs. Three ocelli present. Forewing usually with humeral, marginal and stigmal veins, but some species with postmarginal vein short, others with only humeral vein well developed, other veins being absent, transparent or spurious so that costal cell is open. Front coxa usually with an elongated cavity (coxal corbicula of Ramírez, 1969) on the mesal side (Fig. 98), fenced by a row of bristles on one side. Sternopleural region as illustrated by Grandi (1919, Fig. III). Mesosternum with two depressions (sternal corbiculae of Ramírez, 1969) partially covered by a flap (Fig. 101), so that they open medially, these depressions margined by two rows or groups of hairs, one anteriorly and the other posteriorly

(Fig. 97). Eighth abdominal tergum with spiracles and peritremata small and rounded. Ninth segment with two socii, each provided with a variable number of generally elongate setae. Ovipositor usually longer than length of abdomen.

Male: Head with a dorsal angular invagination which narrows caudally. Eyes laterodorsal and on extreme anterior portion of head. Dorsal surface of head covered with scattered small hairs. Antenna with four free segments (six segmented in *B. astoma* which lacks maxillolabial complex and mouth); last segment divided into three distinct parts, proximal and distal parts much smaller than medial; third segment sometimes also with a division. Maxillolabial complex usually present. Pronotum well differentiated; mesonotum, metanotum and propodeum fused dorsally. Sternopleural region as illustrated by Grandi (1919, Fig. XIII). Anterior tarsi two segmented, second segment with weak divisions. Middle leg well developed. Tenth abdominal segment without socii.

KEY TO DESCRIBED AGAONID WASPS FROM COSTA RICA

1. Front wing with incomplete humeral vein; marginal, stigmal and postmarginal veins absent; costal cell open 2
— Front wing with complete humeral vein; marginal and stigmal veins present, some species also with postmarginal; costal cell closed 3
2. Coxal and sternal corbiculae absent ..... *Tetrapus costaricanus*
— Coxal and sternal corbiculae present 4
3. Front wing with postmarginal vein atrophied 5
— Front wing with postmarginal vein present 6
4. Maxilla with 3 medial bristles ..... *Blastophaga aguilari*
— Maxilla with 4 medial bristles ..... *B. torresi*
5. Front leg with coxal corbicula 7
— Front leg without coxal corbicula 8
6. Last 7 flagellomeres with flat projecting bristles; front tibia with 3 apical teeth in anterodorsal side; apical process of hind tibia with 5 teeth ..... *B. urbanae*
— Last 7 flagellomeres with only slender bristles; front tibia with 2 teeth in anterodorsal side; apical process of hind tibia tridentate ..... *B. astoma*
7. Mandible with very small median and a very long projecting apical tooth (Fig. 118) ..... *B. jimenezi*
— Mandible with a medium size median tooth, apical tooth short, projecting 9
8. Body honey colored, head and thoraxic dorsum blackish; abdominal dorsum with a broad blackish spot. Coxae and femora honey colored ..... *B. mariae*
— Body, coxae and femora blackish ..... *B. carlosi*
9. Apical process of hind tibia with 1 or 2 teeth 10
— Apical process of hind tibia with 3 or more teeth 11
10. Apical process of hind tibia with 1 tooth; maxilla without median but with 2 subapical bristles ..... *B. ileanae*
— Apical process of hind tibia bidentate; maxilla with 1 median and 1 subapical bristle ..... *B. orozcoi*

11. Apical process of hind tibia annular with 4 large and 6 small teeth; maxilla with 2 or 3 median bristles ..... *B. estherae*
— Apical process of hind tibia not annular, with 3 teeth; maxilla without or with 1 median bristle 12
12. Maxilla without median bristle ..... *B. tonduzi*
— Maxilla with 1 medial bristle ..... *B. standleyi*

Descriptions of Seven New Species of Blastophaga from Central America and Venezuela

For all descriptions the characters are numbered to facilitate ready comparison among the descriptions. Certain measurements of all seven species are given in Tables 2 and 3.

Holotypes and allotypes will be placed in the collection of the U.S. National Museum. Paratypes will be in the Snow Entomological Museum, University of Kansas, and the collection of the author. Additional specimens are deposited in the British Museum (Natural History), in the Istituto di Entomologia, Università degli Studi di Bologna and in the Rijksmuseum van Natuurlijke Historie, Lieden.

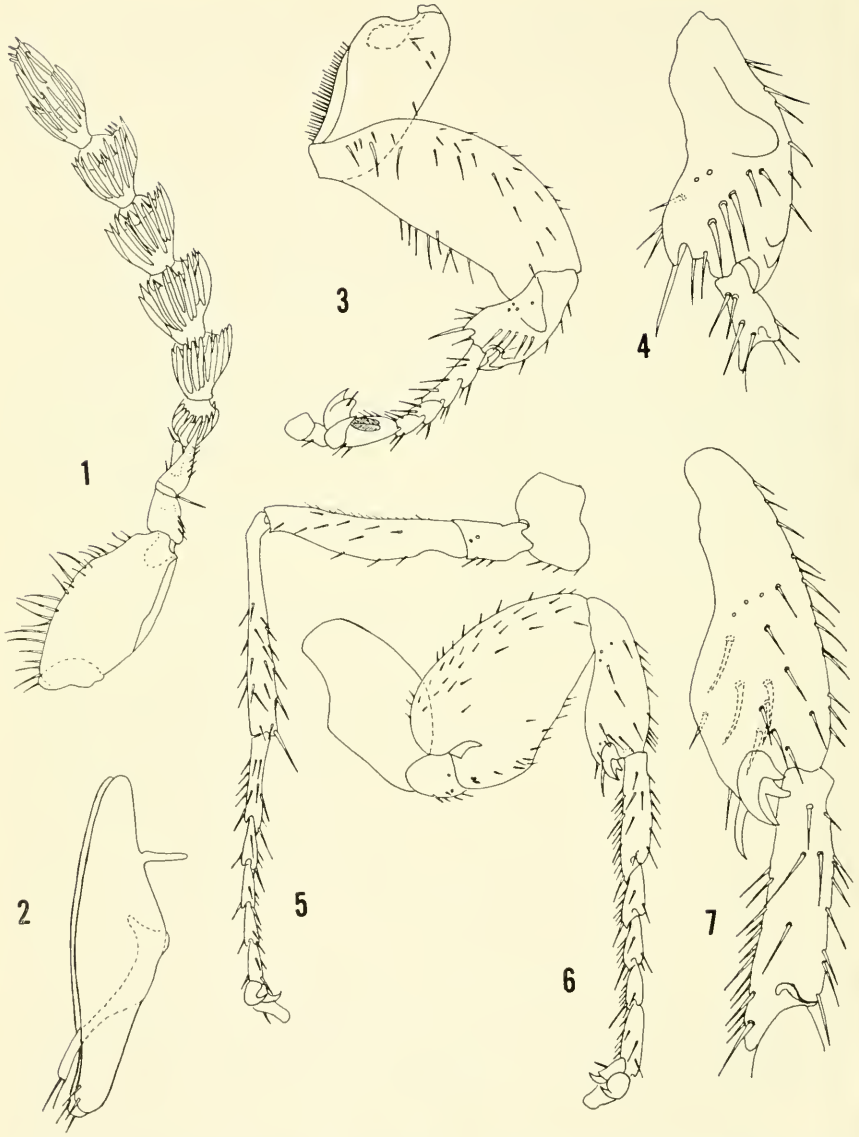
Blastophaga cumanensis new species

(Figs. 1-14, 97, 98)

Comparative comments. Female: This is the largest of the new species described. Its maxilla (Fig. 2) lacks median bristles as does *B. ileanae* (Fig. 91), but the former can be distinguished because of its size (body length 2.10 mm), its labium which has two apical bristles (one in *B. ileanae*), and because it has three teeth on the apical process of the hind tibia (Fig. 7) whereas *ileanae* has only one (Fig. 96). The front tibia in *B. cumanensis* has three anterodorsal apical teeth (Fig. 4) while *B. ileanae* has only two apical teeth (Fig. 93). *Male:* The mesosomal dorsum is quite narrow anteriorly in relation to the rest of the structure (Fig. 14). Its hind tibia has four medium sized and two small apical teeth (Fig. 13).

Types: Holotype female, specimen No. 1 (slide 921). Female paratypes: No. 2 (922), No. 3 (923), No. 4 (924), No. 5 (925), No. 6 (926-927), No. 7 (928-929-930-931), No. 8 (932). Allotype male, No. 9 (933). Male paratypes: No. 10 (934), No. 11 (935), No. 12 (936), No. 13 (937), No. 14 (938). *Host: Ficus* sp. (*Ficus* No. 4 of Venezuela). *Locality:* Cumaná, 15 Km along route to Puerto La Cruz, Estado Sucre, Venezuela. *Date:* June 27, 1966. Many other specimens of both sexes are preserved in vial No. 431.

Female: (1) Body length 2.10 mm; ovipositor 1.00 mm. (2) Head and dorsum of body blackish. (3) Scape, pedicel, and segment 1 of flagellum honey colored, rest of flagellum brownish. (4) Sides and venter of body lighter than dorsum. (5) Coxae and femora colored as sides of body, but with dorsal sides of femora darker; rest of legs honey colored. (6) Head



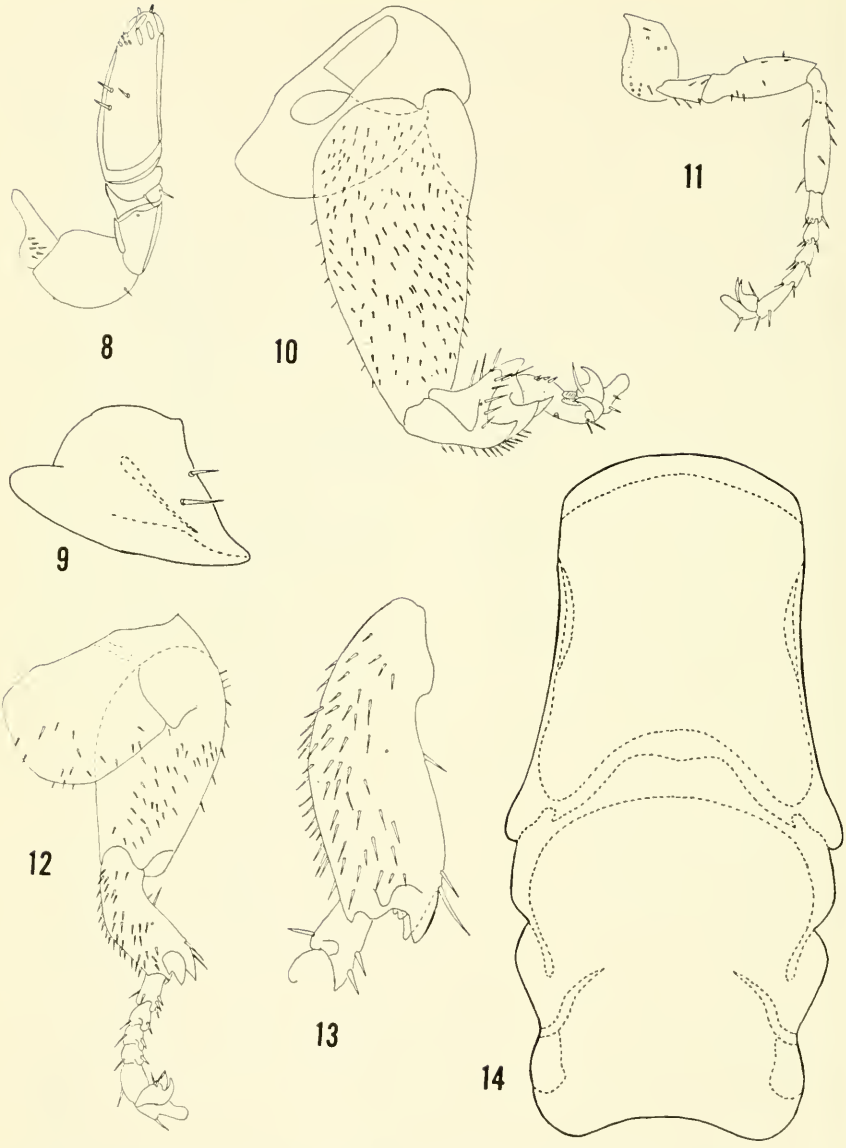
FIGS. 1-7. *Blastophaga cumanensis. Female:* **1,** antenna; **2,** maxillo-labial complex; **3,** front leg; **4,** front tibia; **5,** middle leg; **6,** hind leg; **7,** hind tibia.

subtriangular, slightly wider than long, posterior side slightly concave. (7) Compound eye as long as gena. (8) Premandibular projection without bristles; clypeus with 24 or 26 setae; epistomal margin with submedial lobes very prominent, medial lobe smaller than submedial ones. (9) Antennae

(Fig. 1) with scape suboval, length less than twice width; flagellomere 1 with apical process slightly surpassing apex of 2; 2 longer than wide; 3 to 8 with longitudinal sensilla; 3 wider than long, with 6 or 7 sensilla; 4 wider than long, with 8 or 9 sensilla; 5 larger than 4, wider than long, with 11 sensilla; 6 and 7 wider than long but narrower than 5, with 10 sensilla; 8 narrower than 7, with 9 sensilla; 9 subconical, much longer than wide, with 6 longitudinal and 3 circular sensilla. (10) Mandible (Fig. 106) bidentate, as long as wide, with 5 or 6 ventral ridges. (11) Mandibular appendage with 6 lamellae. (12) Maxilla (Fig. 2) with no medial bristles and 2 subapical bristles. (13) Labium (Fig. 2) with 2 apical bristles. (14) Front leg (Fig. 3): coxa with corbicula (Fig. 98), coxal length twice width; femoral length twice width; tibial length more than twice width, tibia with 3 apical teeth located anteriorly and one posteriorly (Fig. 4); tarsus with segment 1 shorter than 5; 2, 3, and 4 diminishing progressively in length, each shorter than 1. (15) Middle leg (Fig. 5): coxal width 1.5 × length; femoral length 4 × width; tibial length 6 × width; tarsus with segment 1 longest, 2 and 3 of equal length, longer than 5; 4 shorter than 5. (16) Hind leg (Fig. 6): coxal length less than twice width; femoral length 1.5 × width; tibial length more than twice width, apical process tridentate (Fig. 7); tarsus with segment 1 longest, segments 2 and 3 of equal length, 4 the smallest, 5 longer than 2. (17) Front wing length slightly more than twice width, humeral vein with 3 pustules, marginal much shorter than stigmal, stigmal with 4 pustules, postmarginal atrophied. (18) Hind wing length 4 × width. (19) Mesosternum: sternal corbicula (Fig. 97) with 7 to 9 hairs in anterior row and 7 or 8 located posteriorly; sternum with 13 or 14 hairs on each side.

Male: (20) Head slightly wider than long. (21) Antenna as in Figure 8. (22) Maxillo-labial complex lobiform with 3 apical lobelets, middle one with 2 apical bristles, main structure with 2 medial bristles. Mandible as in Figure 9. (23) Front leg (Fig. 10): coxal width almost 2 × length; femoral length almost twice width; tibial length twice width, 5 apical teeth (Fig. 11); tarsal segment 1 shorter than 2. (24) Middle leg (Fig. 11): coxa much wider than long; femoral length 3 × width; tibial length 4 × width; tarsus longer than tibia, segment 1 longer than 2; 2 and 3 equal length, 4 smallest, 5 longest. (25) Hind leg (Fig. 12): coxa much wider than long; femur much narrower than coxa, length twice width; tibia with 6 apical teeth (Fig. 13); tarsus shorter than tibia, segment 1 shorter than 5, 2 slightly longer than 3; 4 as long as 3 and fused to 5, 5 longest. (26) Mesosomal dorsum (Fig. 14) with length 1.40 mm, maximum width 0.74 mm, anterior width 0.45 mm, posterior width 0.48 mm.

This species is named for the location where it was studied, the town of Cumaná, Sucre, Venezuela.



FIGS. 8-14. *Blastophaga cumanensis*. *Male:* **8,** antenna; **9,** mandible; **10,** front leg; **11,** middle leg; **12,** hind leg (ventral view); **13,** hind tibia; **14,** mesosomal dorsum.

Blastophaga mariae new species

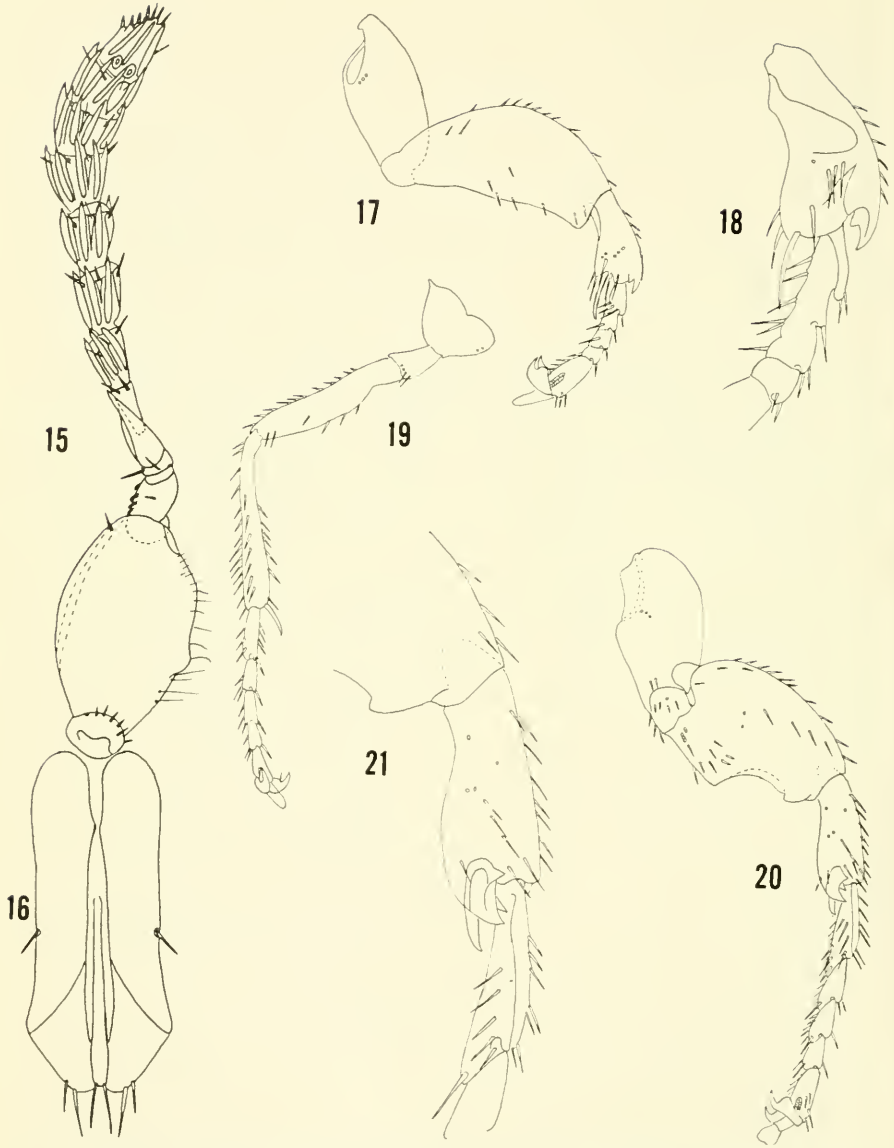
(Figs. 15-29, 102)

Comparative comments. *Female:* In size this is the second largest among newly described species (body length 1.70 mm). Its maxilla (Fig. 16) pos-

sesses 1 medial and 2 subapical bristles as in *B. carlosi* (Fig. 31) and *B. Standleyi* (Fig. 61) but *B. mariae* differs from these two species especially in coloration. The legs, venter and sides of the body are honey colored, the head, thoracic dorsum and mesal section of the abdominal dorsum blackish. The bodies of *B. carlosi* and *B. standleyi* are almost completely black. *B. mariae* differs also from *B. carlosi* by the 3 teeth on the anterodorsal side of the front tibia (Fig. 18), where *B. carlosi* possesses only 2. *Male:* Smaller than that of *B. cumanensis,* with the mesosomal dorsum (Fig. 29) much wider anteriorly than in the latter (Fig. 14). The hind tibia has 5 large apical teeth (Fig. 28).

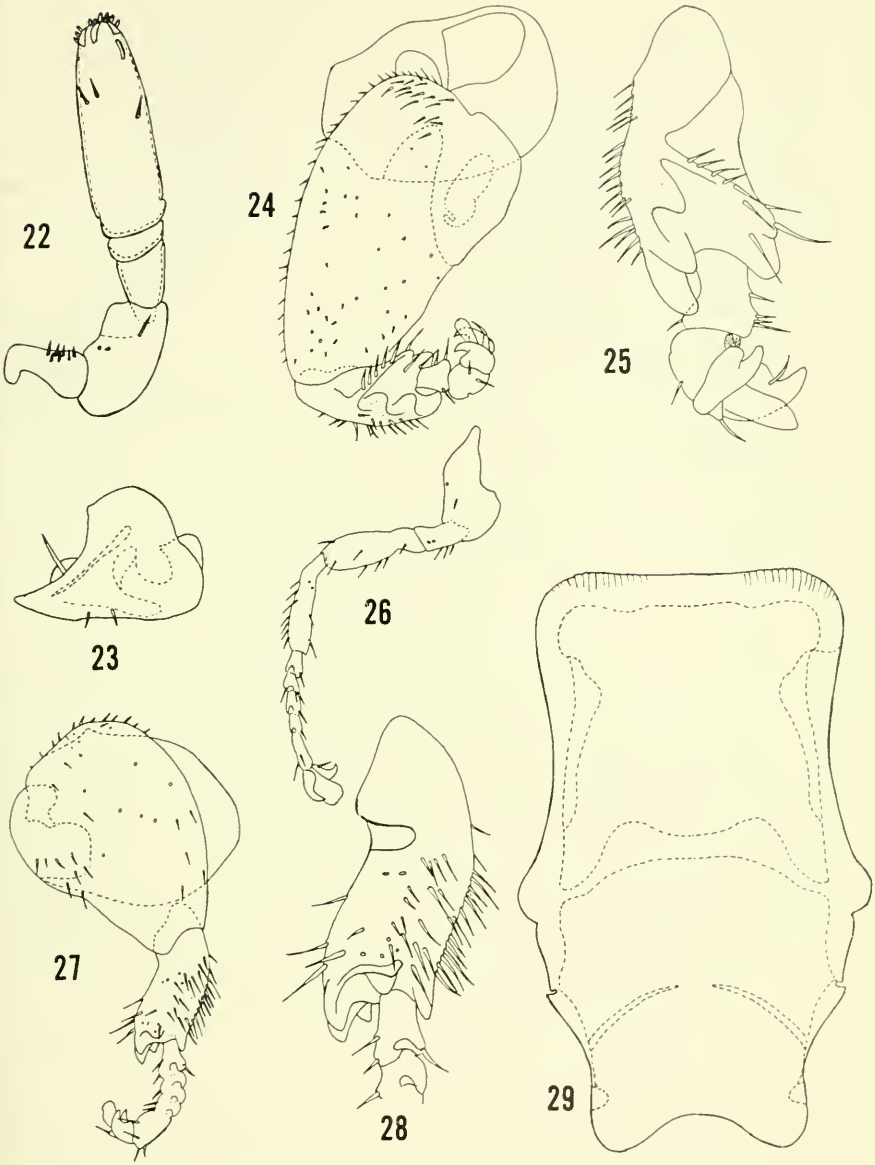
Types: Holotype female, specimen No. 1 (slides 944-945-946). Female paratypes: No. 2 (900-901), No. 3 (947), No. 4 (949), No. 5 (950), No. 6 (951-952-953). Allotype male, No. 7 (1292). Male paratypes: No. 8 (954), No. 9 (955). *Host: F. tuerckheimii* Stand. *Locality:* San Jerónimo de Moravia, San José, Costa Rica. *Date:* May 1, 1964. Many other specimens of both sexes are preserved in vial No. 149. Other specimens were taken at each of the localities for this *Ficus* listed in Table 1.

Female: (1) Body length 1.70 mm; ovipositor length 1.02 mm. (2) Head and dorsum of thorax blackish brown. (3) Scape, pedicel, and segment 1 of flagellum honey colored, rest of flagellum brownish. (4) Sides of body, venter of thorax and abdomen honey colored, medial section of abdominal terga 1 to 5 broadly blackish brown. (5) Legs honey colored, like sides of body. (6) Head (Fig. 102) subquadrangular, slightly longer than wide, posterior side concave. (7) Compound eye shorter than gena. (8) Premandibular projection with 3 stout short bristles; clypeus with 6 setae; epistomal margin almost straight, without submedial lobes, medial lobe very small (Fig. 102). (9) Antenna (Fig. 15) with scape suboval, length almost twice width; flagellomere 1 with apical process reaching apex of 2; 2 much longer than wide; 3 to 8 with longitudinal sensilla; 3 longer than wide, with 2 or 3 sensilla; 4 longer than wide, longer than 5, with 3 or 4 sensilla; 5 slightly longer than wide, with 5 sensilla; 6 as long as broad, with 5 sensilla; 7 and 8 shorter than 6, 8 narrower than 7, each with 5 sensilla; 9 subconical, with 3 longitudinal and 2 round sensilla. (10) Mandible (Fig. 107) bidentate, slightly wider than long, with 8 or 9 ventral ridges. (11) Mandibular appendage with 9 lamellae (some specimens with 7, 8, or 10). (12) Maxilla (Fig. 16) with 1 medial and 2 subapical bristles. (13) Labium (Fig. 16) with 2 apical bristles. (14) Front leg (Fig. 17): coxa without corbicula, length twice width; femoral length more than twice width; tibial length twice width, tibia with 3 apical teeth located anteriorly and 1 small posteriorly (Fig. 18); tarus with segment 1 longer than 2; 2, 3 and 4 of equal length; 5 longest. (15) Middle leg (Fig. 19): coxal width 2.5 $\times$ length; femoral length 3.5 $\times$ width; tibial length 5 $\times$ width; tarsus with



FIGS. 15-21. *Blastophaga mariae*. *Female:* **15**, antenna; **16**, maxillo-labial complex; **17**, front leg; **18**, front tibia; **19**, middle leg; **20**, hind leg; **21**, hind tibia.

segment 1 longest, 2 longer than 3, 3 longer than 4, 4 shortest, 5 slightly shorter than 1. (16) Hind leg (Fig. 20): coxal length 1.4 × width; femoral length less than 1.5 × width; tibial length 3 × width, apical process tridentate (Fig. 21); tarsus with segment 1 longest, 2, 3, and 4 progressively



FIGS. 22-29. *Blastophaga mariae*. *Male:* 22, antenna; 23, mandible; 24, front leg; 25, front tibia; 26, middle leg; 27, hind leg; 28, hind tibia; 29, mesosomal dorsum.

diminishing in length, 5 longer than 2. (17) Front wing length more than twice width, humeral vein with 3 pustules, marginal slightly shorter than stigmal, stigmal with 3 pustules, postmarginal atrophied. (18) Hind wing length more than 3 × width. (19) Mesosternum: sternal corbicula with 5

to 8 hairs in anterior row and 1 or 2 located posteriorly; sternum with 5 or 6 hairs on each side.

Male: (20) Head wider than long. (21) Antenna as in Figure 22. (22) Maxillo-labial complex lobiform with 1 apical (some specimens 2) and 2 subapical bristles. Mandible as in Figure 23. (23) Front leg (Fig. 24): coxa much wider than long; femoral length almost twice width; tibial length twice width, 5 apical teeth (Fig. 25); tarsus of 2 subequal segments. (24) Middle leg (Fig. 26): coxa much wider than long, femoral length twice width; tibial length 4 × width; tarsus slightly longer than tibia, segment 1 longer than 2; 3 and 4 of equal length, longer than 2; 5 longest. (25) Hind leg (Fig. 27): coxa wider than long; femoral width same as coxa; tibia with 5 apical teeth (Fig. 28); tarsus shorter than tibia, segment 1 longer than 2; 2 and 3 equal length, 4 shortest; 5 longest. (26) Mesosomal dorsum (Fig. 29) with length 1.20 mm, maximum width 0.72 mm, anterior width 0.60 mm, posterior width 0.45 mm.

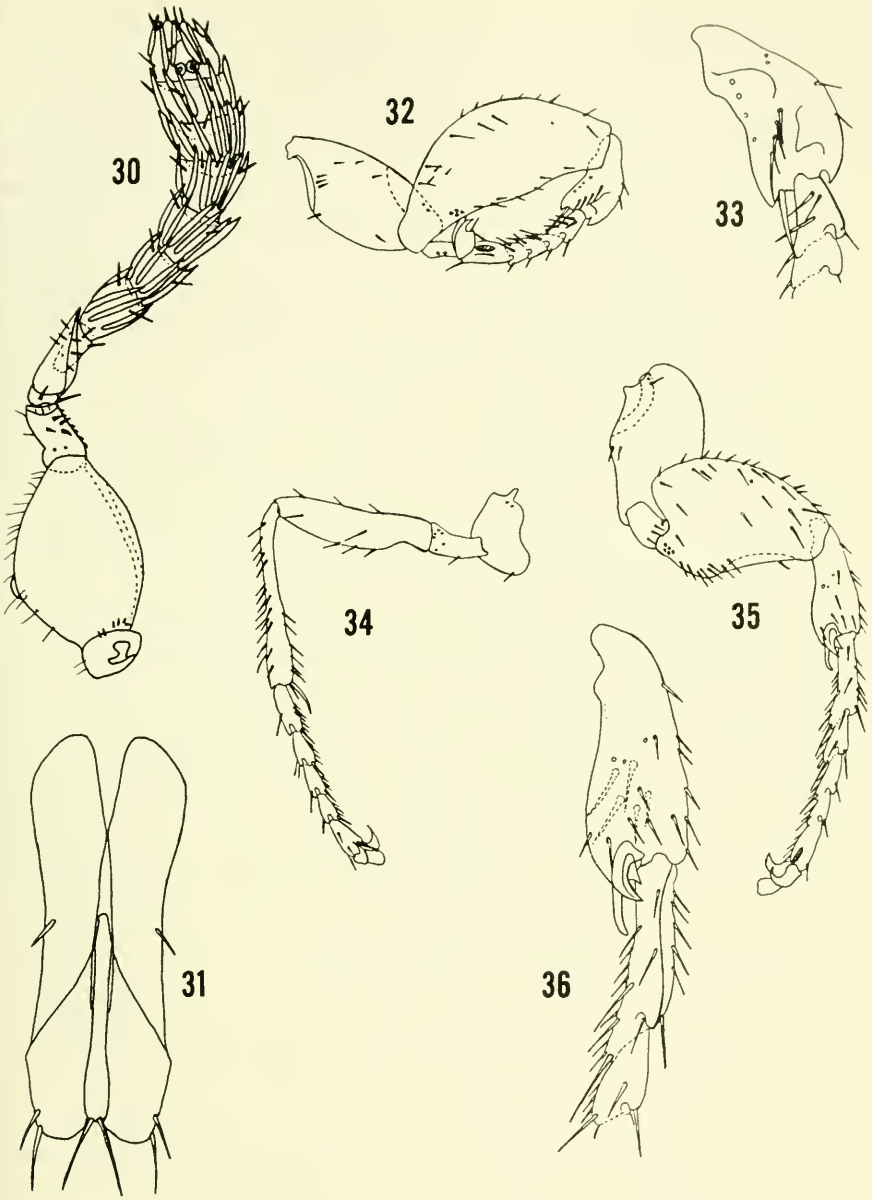
This species is named for Mrs. Mary H. Michener, formerly editor of the Journal of the Kansas Entomological Society.

Blastophaga carlosi new species

(Figs. 30-44, 99, 100, 103, 112)

Comparative comment. *Female:* This is the third species in size among species described (body length 1.67 mm). It is quite similar to *B. mariae.* Neither possesses coxal corbiculae (Fig. 100) and both have very reduced sternal corbiculae (Fig. 99). *B. carlosi* differs from *B. mariae* by its black color and some minor morphological characters. The antenna of *B. carlosi* (Fig. 30) has more sensilla per flagellomere; the head of *B. carlosi* is smaller (Fig. 103) with the epistomal margin bearing more prominent submedial and medial lobes than in *B. mariae,* in which this margin is almost straight (Fig. 102). The mandible in *B. carlosi* is smaller and possesses fewer lamellae (8-9) on the mandibular appendage (Fig. 112); *B. mariae* usually possesses from 8 to 10 (Fig. 107). Both species usually develop side by side in the same receptacles of *F. tuerckheimii,* or synchronously in different receptacles of the same fig tree. Male: Slightly smaller than male of *B. mariae,* its mesosomal dorsum (Fig. 44) very similar to that of *B. mariae* (Fig. 29). The front tibia (Fig. 40) differs from that of *B. mariae* (Fig. 25) because the apical tooth of the posterodorsal side is more pointed. The hind tibia has 5 large apical teeth (Fig. 43).

Types: Holotype female, specimen No. 1 (slide 1281). Female paratypes: No. 2 (886-887), No. 3 (898-899), No. 4 (940), No. 5 (941-942), No. 6 (1284). Allotype male, specimen No. 7 (886). Male paratypes: No. 8 (678), No. 9 (679-880), No. 10 (881-882), No. 11 (883-884), No. 12 (942), No. 13 (943). *Host: F. tuerckheimii* Stand. *Locality:* San Jerónimo de Moravia, San José,

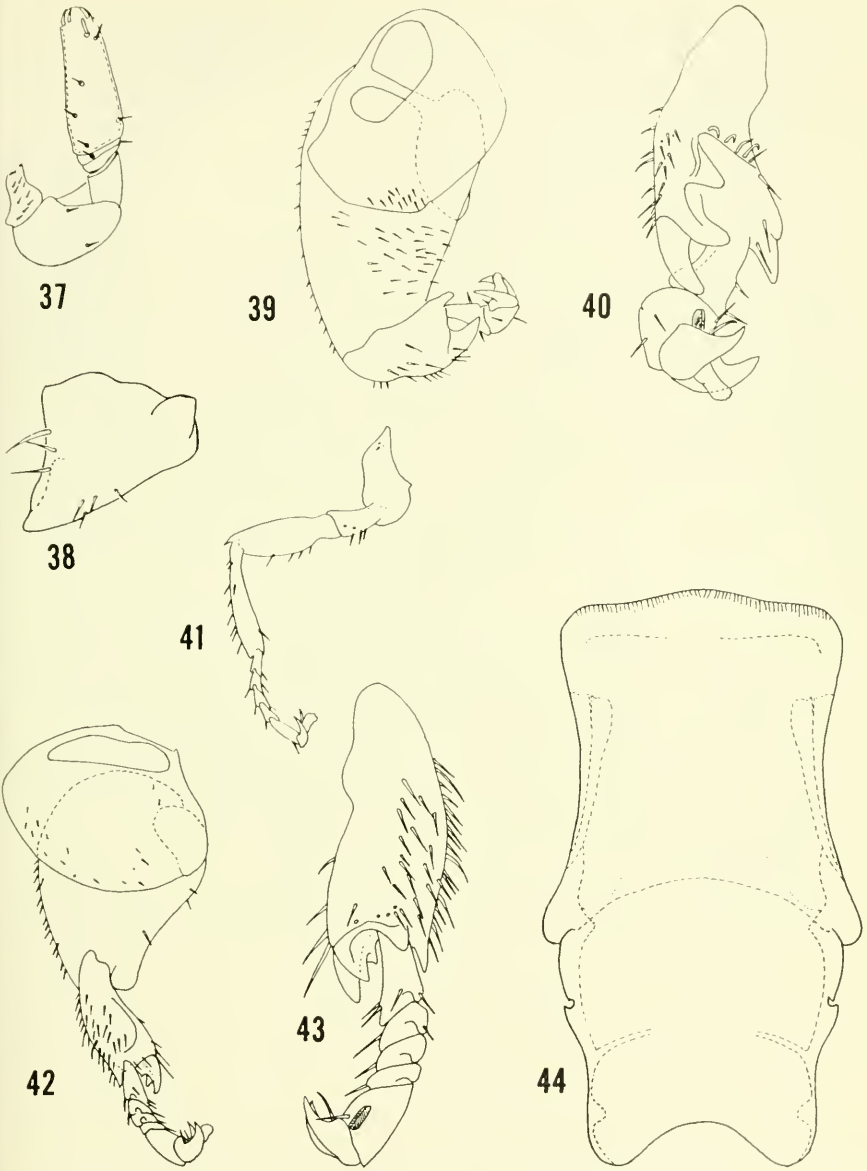


FIGS. 30-36. *Blastophaga carlosi*. *Female:* 30, antenna; 31, maxillo-labial complex; 32, front leg; 33, front tibia; 34, middle leg; 35, hind leg; 36, hind tibia.

Costa Rica. *Date:* May 1, 1964. Many other specimens of both sexes are preserved in vial No. 159. Other specimens were taken at each of the localities for this *Ficus* listed in Table 1.

Female: (1) Body length 1.67 mm; ovipositor length 1.09 mm. (2) Head, thorax and abdominal venter black. (3) Scape, pedicel and segment 1 of flagellum honey colored, rest of flagellum brownish. (4) Sides of body and abdominal dorsum lighter than rest of body. (5) Coxae and femora black; tibiae and tarsi honey colored. (6) Head (Fig. 103) subquadrangular, slightly longer than wide, almost flat posteriorly. (7) Compound eye shorter than gena. (8) Premandibular projection with 3 or 4 short stout bristles; clypeus with 6 setae; epistomal margin with wide but slightly prominent submedial lobes, medial lobe conspicuous (Fig. 103). (9) Antenna (Fig. 30) with scape suboval, almost twice as long as wide; flagellomere 1 with apical process surpassing apex of 2, 2 much longer than wide; 3 to 8 with longitudinal sensilla; 3 longer than wide, with 4 or 5 sensilla; 4 slightly longer than wide, with 5 sensilla; 5 and 6 as broad as long, each with 6 or 7 sensilla; 8 much wider than long, with 7 sensilla; 9 subconical, with 5 longitudinal and 2 circular sensilla. (10) Mandible (Fig. 112) bidentate, slightly wider than long, with 8 or 9 ventral ridges. (11) Mandibular appendage with 8 or 9 lamellae (some specimens 7). (12) Maxilla (Fig. 31) with 1 median and 2 subapical bristles. (13) Labium (Fig. 31) with 2 apical bristles. (14) Front leg (Fig. 32): coxa without corbicula (Fig. 100), length twice width; femoral length more than twice width; tibial length twice width, tibia with 2 apical teeth located anteriorly and 1 posteriorly (Fig. 33); tarsus with segment 1 shorter than 5, segment 2 slightly shorter than 3; 3 and 4 of equal length, 5 longest. (15) Middle leg (Fig. 34): coxal width 1.5 × length; femoral length 4 × width; tibial length 5 × width; tarsus with segment 1 longest, 2 and 3 equal length, 4 shortest, 5 longer than 2. (16) Hind leg (Fig. 35): coxal length slightly more than 1.5 × width; femoral length more than 1.5 × width; tibial length 3 × width, apical process tridentate (Fig. 36); tarsus with segment 1 longest, 2 and 3 equal length, 4 smallest, 5 longer than 2. (17) Front wing length twice width, humeral vein with 3 pustules, marginal slightly shorter than stigmal, stigmal with 3 pustules, postmarginal atrophied. (18) Hind wing length 3 × width. (19) Mesosternum: sternal corbicula with 7 hairs in anterior row (some specimens with 6 or 8) and 2 located posteriorly; sternum with 4 or 5 hairs on each side (Fig. 99).

Male: (20) Head longer than wide. (21) Antenna as in Figure 37. (22) Maxillo-labial complex lobiform with 1 apical and 2 medial bristles. Mandible as in Figure 38. (23) Front leg (Fig. 39): coxal width twice length; femoral length almost twice width; tibial length twice width, 5 apical teeth (Fig. 40); tarsus of 2 segments of approximately equal length. (24) Middle leg (Fig. 41): coxa longer than wide; femoral length almost twice width; tibial length 4 × width; tarsus as long as tibia, segment 1 longer than 2; 2 smallest, 3 and 4 of equal length, 5 longest. (25) Hind leg (Fig.



FIGS. 37-44. *Blastophaga carlosi*. *Male:* 37, antenna; 38, mandible; 39, front leg (ventral view); 40, front tibia; 41, middle leg; 42, hind leg (ventral view); 43, hind tibia; 44, mesosomal dorsum.

42): coxa slightly wider than long; femur narrower than coxa; tibia with 5 apical teeth (Fig. 43); tarsus shorter than tibia, segment 1 twice as long as 2; 2 and 3 of equal length, and both longer than 4; 5 longest. (26) Mesosomal

dorsum (Fig. 44) with length 1.17 mm, maximum width 0.72 mm, anterior width 0.60 mm, posterior width 0.48 mm.

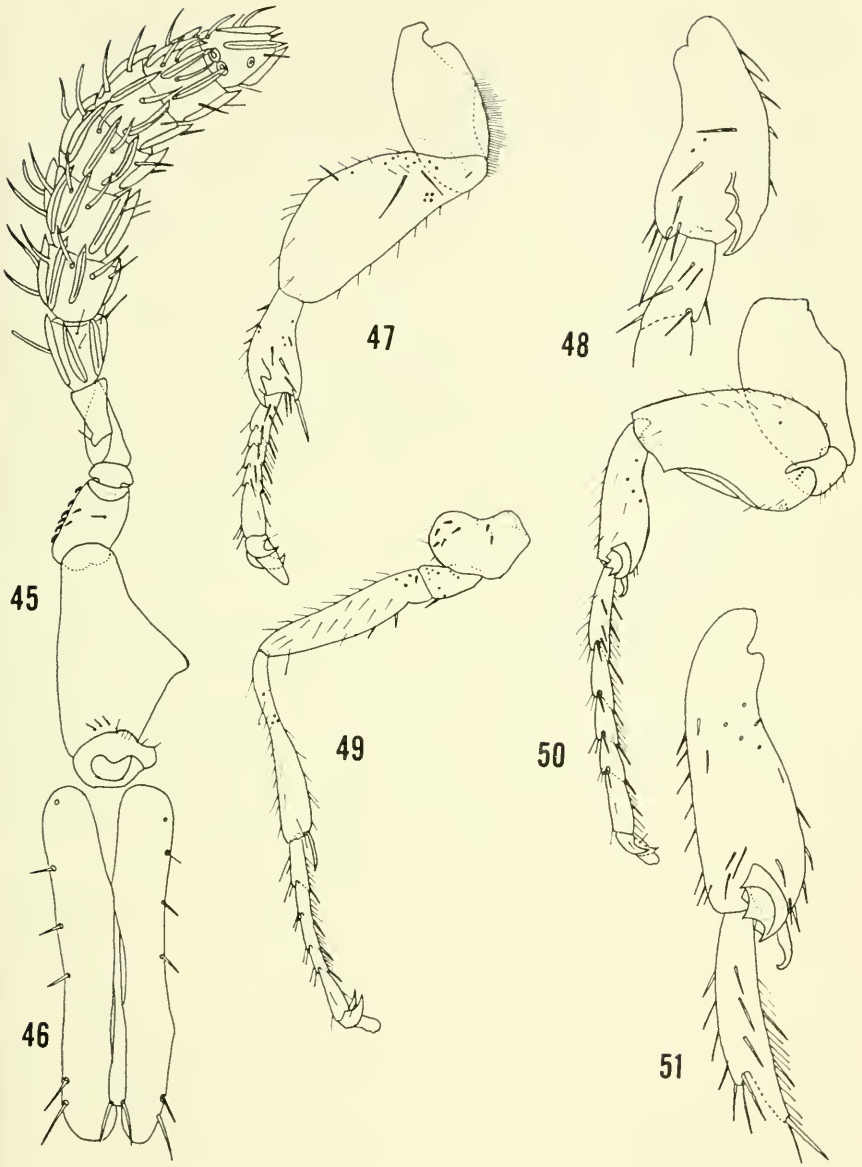
This species is named for my advisor, Dr. Charles D. Michener (University of Kansas).

Blastophaga urbanae new species
(Figs. 45-59, 116)

Comparative comments. *Female:* Much smaller than *B. carlosi* (body length 1.33 mm). This wasp possesses the most characteristic antenna of the group described. Its last 7 flagellomeres possess flat, long, projecting bristles (Fig. 45). Its maxilla has 4 medial (others 1 or none) and 2 subapical bristles (Fig. 46). The front wing has a short postmarginal vein (absent in other described species). Its hind tibia has the apical process with 5 teeth (Fig. 51) (other new species with 3 or less); in this respect *B. urbanae* resembles *B. estherae* Grandi. *Male:* Much smaller than male of *B. carlosi* with mesosomal dorsum quite narrow anteriorly (Fig. 59). The hind tibia has 4 large apical teeth (Fig. 58), other new species have 5 or 6 apical teeth in this position.

Types: Holotype female, specimen No. 1 (slides 875-876-877). Female paratypes: No. 2 (771), No. 3 (912-913-914-915), No. 4 (916-917-918), No. 5 (972-973-974), No. 6 (1035-1036), No. 7 (1406-1407-1408). Allotype male, No. 8 (869-870-871). Male paratypes: No. 9 (867-868), No. 10 (919), No. 11 (920). *Host: F. isophlebia* Stand. *Locality:* Ciruelas, Alajuela, Costa Rica. *Date:* August 20, 1964. Many other specimens of both sexes are preserved in vial No. 48. Other specimens studied were obtained as listed under the host in Table 1.

Female: (1) Body length 1.33 mm; ovipositor 0.68 mm. (2) Head and dorsum of thorax blackish amber. (3) Antenna with scape and pedicel honey colored, rest blackish. (4) Abdominal dorsum and venter of body lighter than rest of body. (5) Front and hind femora blackish, hind femur darker than front femur, rest of legs honey colored. (6) Head subtriangular, wider than long, posterior side concave. (7) Compound eye length equal to length of gena. (8) Premandibular projection with 2 long bristles; clypeus with 8 setae; epistomal margin with prominent, round, submedial lobes, medial lobe round and prominent but smaller than submedial ones. (9) Antenna (Fig. 45) with scape subtriangular, length less than twice width; flagellomere 1 with apical process reaching apex of 2; 2 longer than wide; 3 to 9 with long, projecting, flattened setae and longitudinal sensilla; 3 longer than wide, with 3 or 4 sensilla; 4 wider than long, with 4 sensilla; 5 wider than long, with 5 or 6 sensilla; 6 wider than long, with 5 sensilla; 7 to 9 forming a loose club; 7 shorter than wide, shorter than 6, with 4 or 5 sensilla; 8 as wide as long, with 5 sensilla; 9 subconical, slightly longer than 8, with 3 longitudinal



Figs. 45-51. *Blastophaga urbanae. Female:* **45,** antenna; **46,** maxillo-labial complex; **47,** front leg; **48,** front tibia; **49,** middle leg; **50,** hind leg; **51,** hind tibia.

and 3 round sensilla. (10) Mandible (Fig. 116) bidentate, wider than long, with 10 ventral ridges. (11) Mandibular appendage with 12 lamellae (some specimens with 10 or 11). (12) Maxilla (Fig. 46) with 4 medial (some specimens with 3) and 2 subapical bristles. (13) Labium (Fig. 46) with 2

apical bristles. (14) Front leg (Fig. 47): coxa with corbicula; coxal length less than twice width; femoral length 2.5 × width; tibial length twice width, tibia with 3 apical teeth located anteriorly and 1 posteriorly (Fig. 48); tarsus with segment 1 shorter than 5; 2 and 3 of equal length, 4 shortest. (15) Middle leg (Fig. 49): coxal length 1.7 × width; femoral length almost 4 × width; tibial length 5.6 × width; tarsus with segment 1 longer than 5; 2 and 3 of equal length, 4 shortest. (16) Hind leg (Fig. 50): coxal length twice width; femoral length less than twice width; tibial length 3 × width, apical process with 5 teeth (Fig. 51); tarsus with segment 1 longest, 2 and 3 of equal length, 4 shorter than 3, 5 as long as 2. (17) Front wing length twice width, humeral vein with 3 pustules, marginal shorter than stigmal, stigmal with 3 or 4 pustules, postmarginal present. (18) Hind wing length almost 4 × width. (19) Mesosternum: sternal corbicula with 3 to 5 hairs in anterior row and 5 or 7 located posteriorly; sternum with 13 to 17 hairs on each side.

Male: (20) Head as long as wide. (21) Antenna as in Figure 52. (22) Maxillo-labial complex lobiform, with 2 medial bristles and 3 apical lobelets, middle one with 2 bristles. Mandible as in Figure 53. (23) Front leg (Fig. 54): coxal width 1.5 × length; femoral length more than twice width; tibial length twice width, 5 apical teeth (Fig. 55); tarsal segment 1 shorter than 2. (24) Middle leg (Fig. 56): coxa much wider than long; femoral length twice width; tibial length more than 4 × width; tarsus longer than tibia, segment 1 longer than 2; 2, 3, and 4 of equal length, 5 longest. (25) Hind leg (Fig. 57): coxa wider than long; femur narrower than coxa; tibia with 4 apical teeth (Fig. 58); tarsus longer than tibia, segment 1 shorter than 5; 2, 3, and 4 of equal length. (26) Mesosomal dorsum (Fig. 59) with length 0.90 mm, maximum width 0.49 mm, anterior width 0.36 mm, posterior width 0.33 mm.

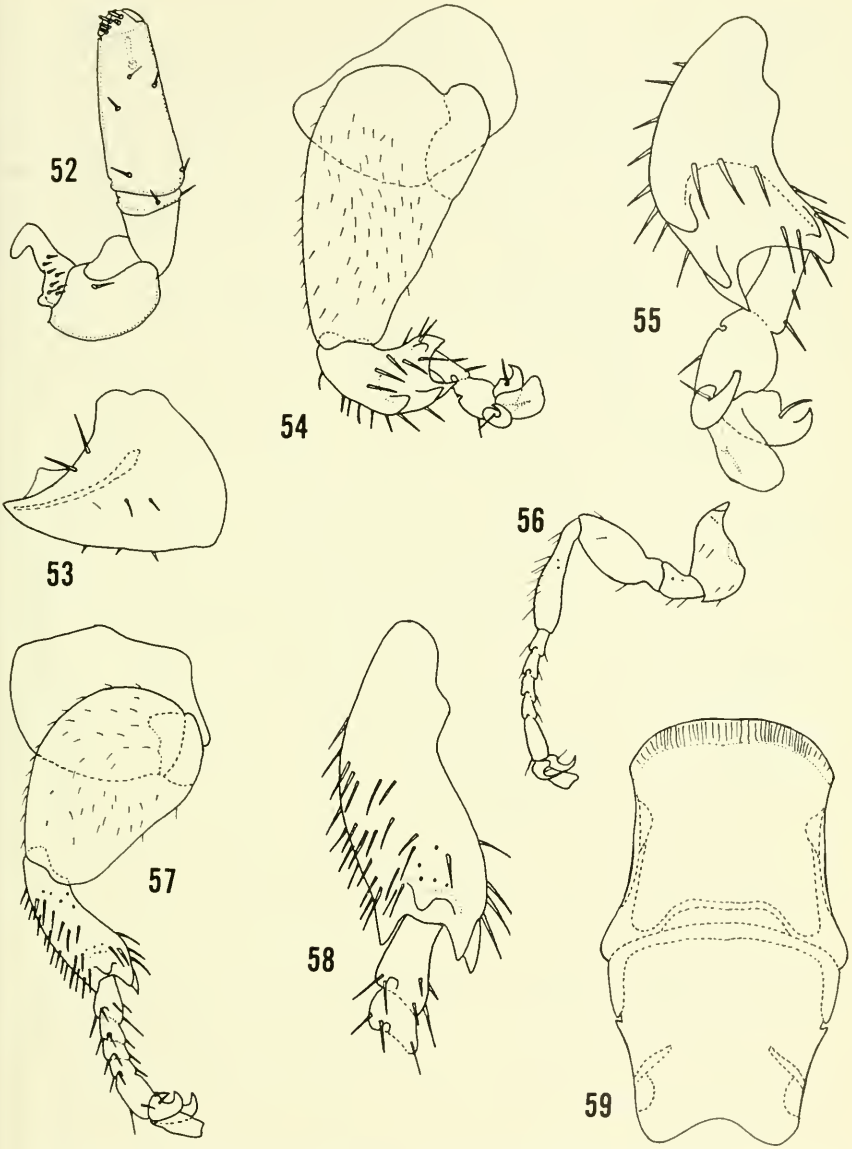
This species is named for my mother Mrs. Urbana Benavides de Ramírez.

Blastophaga standleyi new species

(Fig. 60-74, 119)

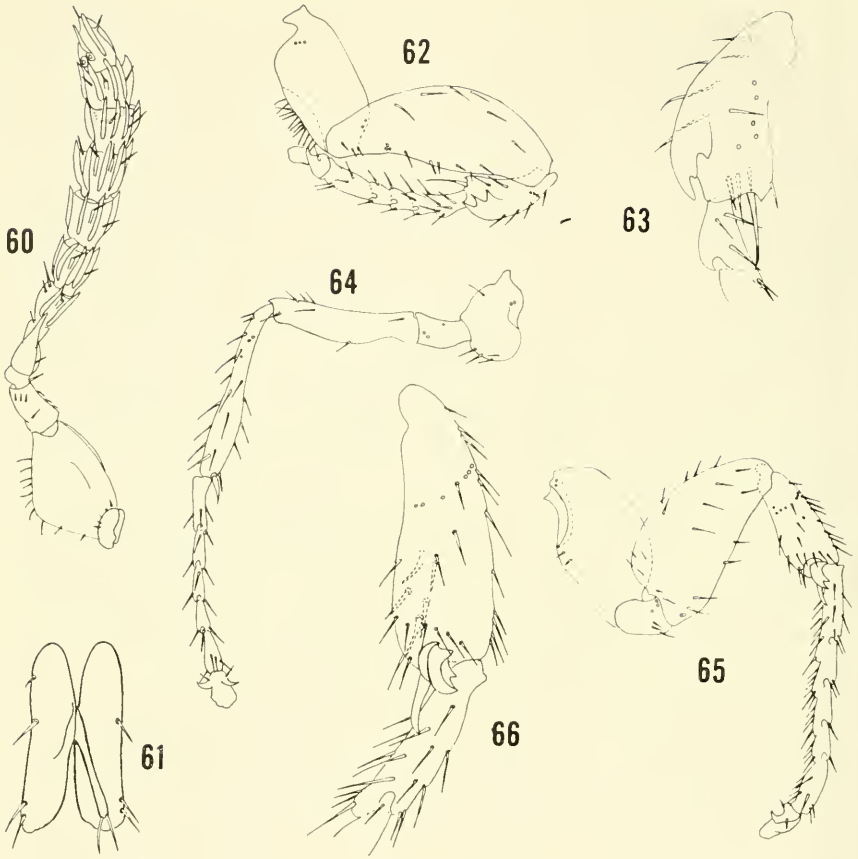
Comparative comments. *Female:* Smaller than *B. urbanae* (body length 1.03 mm). The mandible is bidentate as in the other new species, but the apical tooth is more elongate (Fig. 119), in this respect resembling *B. jimenezi* Grandi. The maxilla has 1 medial and 2 subapical bristles (Fig. 61), and the front tibia has 3 teeth on the anterodorsal side (Fig. 63). In the last two characters *B. standleyi* resembles *B. mariae,* but can be distinguished because of size and the presence of coxal corbiculae. *Male:* Much smaller than male of *B. urbanae* but the conformation of the mesosomal dorsum is quite similar (Fig. 74). The hind tibia has 3 big and 2 small apical teeth (Fig. 73).

Types: Holotype female, specimen No. 1 (slides 1045-1046). Female paratypes: No. 2 (860-861-862), No. 3 (863-864-865-866), No. 4 (1043-1044).



FIGS. 52-59. *Blastophaga urbanae*. *Male:* 52, antenna; 53, mandible; 54, front leg; 55, front tibia; 56, middle leg; 57, hind leg; 58, hind tibia; 59, mesosomal dorsum.

Allotype male, No. 5 (857-858). Male paratypes: No. 6 (849-850), No. 7 (851-852-853), No. 8 (855-856). *Host: F. oerstediana* Stand. *Locality:* La Virgen, Heredia, Costa Rica. *Date:* May 31, 1964. Many other specimens of both sexes are preserved in vial No. 88.



FIGS. 60-66. *Blastophaga standleyi*. *Female:* **60**, antenna; **61**, maxillo-labial complex; **62**, front leg; **63**, front tibia; **64**, middle leg; **65**, hind leg; **66**, hind tibia.

Female: (1) Body length 1.03 mm; ovipositor 0.56 mm. (2) Head blackish. (3) Scape and pedicel honey colored, rest of antenna blackish. (4) Dorsum of thorax blackish amber, abdominal dorsum and venter lighter than rest of body. (5) Front and hind coxae and femora blackish, front femur lighter than hind; rest of legs honey colored. (6) Head subhemispherical, slightly wider than long, posterior side almost straight. (7) Compound eye longer than gena. (8) Premandibular projection with 2 long bristles; clypeus with 8 setae; epistomal margin with prominent submedial lobes, medial lobe prominent but more acute than submedial ones. (9) Antenna (Fig. 60) with scape suboval, length less than twice width; flagellomere 1 with apical process surpassing apex of 2; 2 length less than twice width; 3 to 8 with longitudinal sensilla; 3 longer than wide, with 2 sensilla; 4 slightly longer than wide, with 4 sensilla; 5 to 7 subequal, wider than long,

each one with 4 or 5 sensilla; 8 narrower than 7, with 5 sensilla; 9 longer than wide, with 2 or 3 longitudinal and 2 circular sensilla (in some specimens 3). (10) Mandible (Fig. 119) bidentate, slightly wider than long, with 8 or 9 ventral ridges. (11) Mandibular appendage with 7 lamellae. (12) Maxilla (Fig. 61) with 1 median and 2 subapical bristles. (13) Labium (Fig. 61) with 2 apical bristles. (14) Front leg (Fig. 62): coxa with corbicula, coxal length more than twice width; femoral length almost 3 × width; tibial length more than twice width, tibia with 3 apical teeth anteriorly and 1 posteriorly (Fig. 63); tarsus with segment 1 longer than 2; 2 longer than 3; 3 and 4 of equal length, 5 longest. (15) Middle leg (Fig. 64): coxal width twice length; femoral length more than 4 × width; tibial length 7 × width; tarsus with segment 1 longest, 2, 3, and 4 of equal length, 5 longer than 4. (16) Hind leg (Fig. 65): coxal length 1.75 × width; femoral length 1.5 × width; tibial length 3 × width, apical process tridentate (Fig. 66); tarsus with segment 1 longest, 2 and 3 of equal length, 4 smallest, 5 longer than 2. (17) Front wing length slightly more than twice width, humeral vein with 3 pustules, marginal shorter than stigmal, stigmal with 4 pustules, postmarginal atrophied. (18) Hind wing length less than 4 × width. (19) Mesosternum: sternal corbicula with 6 or 7 hairs in anterior row and 3 or 5 hairs located posteriorly; sternum with 5 hairs on each side.

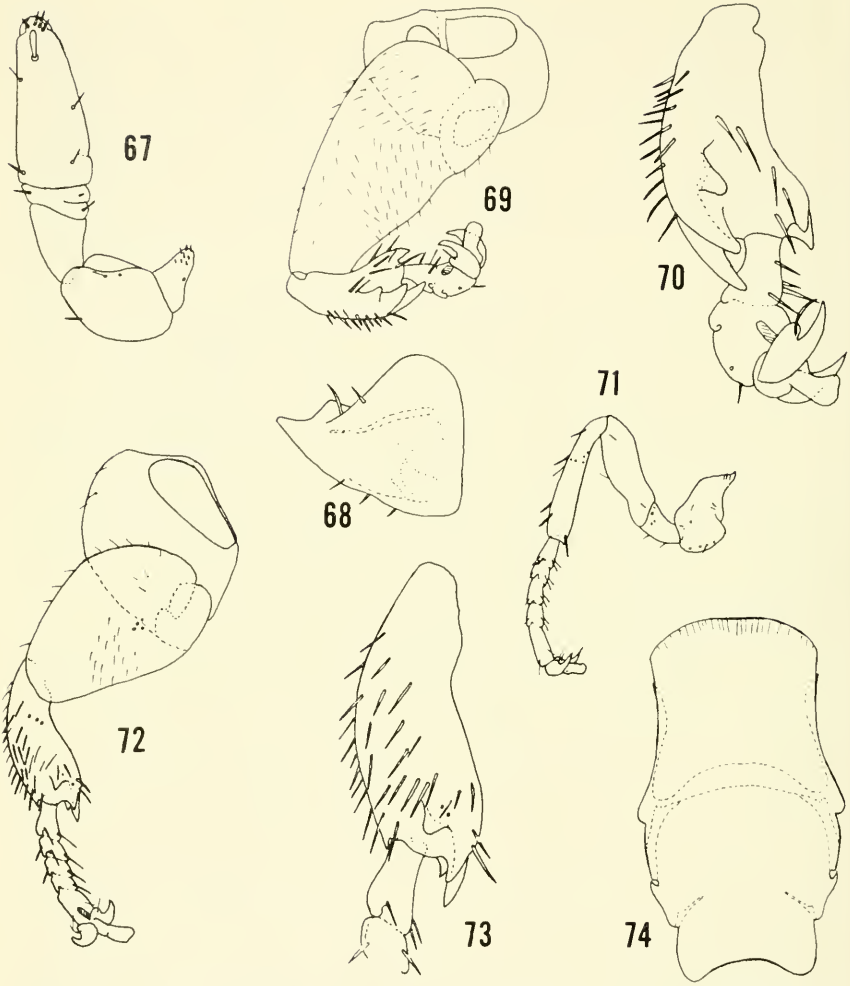
Male: (20) Head as long as wide. (21) Antenna as in Figure 67. (22) Maxillo-labial complex lobiform with 2 apical bristles. Mandible as in Figure 68. (23) Front leg (Fig. 69): coxal width 1.5 × length; femoral length 1.75 × width; tibial length more than twice width, 5 apical teeth (Fig. 70); tarsal segment 1 shorter than 2. (24) Middle leg (Fig. 71): coxa longer than wide; femoral length 2.5 × width, tibial length 6 × width; tarsus longer than tibia, segment 1 longer than 2, 2 smallest, 3 and 4 of equal length, 5 longest. (25) Hind leg (Fig. 72): coxa wider than long; femur narrower than coxa, length 1.6 × width; tibia with 5 apical teeth (Fig. 73) (in some specimens 6); tarsus as long as tibia, segment 1 shorter than 5; 2, 3, and 4 diminishing progressively in length. (26) Mesosomal dorsum (Fig. 74) with length 0.78 mm, maximum width 0.40 mm, anterior width 0.30 mm, posterior width 0.27 mm.

This species is named for the late plant taxonomist, Paul C. Standley, in recognition of his extensive work on Central American figs and other plants.

Blastophaga orozcoi new species

(Figs. 75-89, 120)

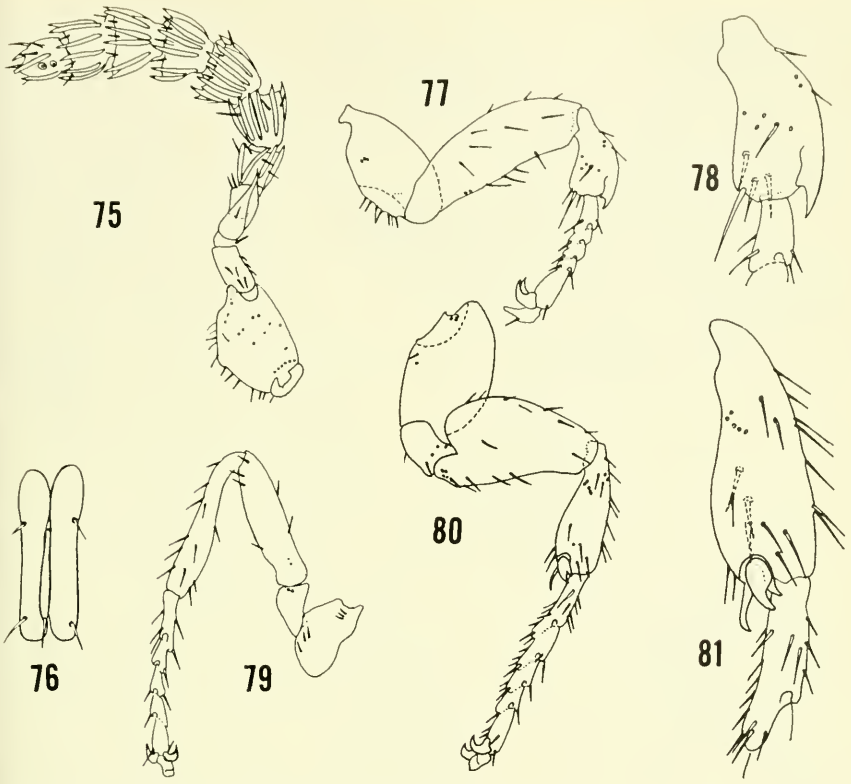
Comparative comments. *Female:* Smaller than *B. standleyi* (body length 0.94 mm). It can be distinguished from it because the maxilla has only 1 subapical bristle (Fig. 76) (*B. standleyi* has 2). The labium has 1 bristle while *B. standleyi* has 2. Its front tibia has 2 apical teeth on the anterodorsal



FIGS. 67-74. *Blastophaga standleyi. Male:* **67,** antenna; **68,** mandible; **69,** front leg; **70,** front tibia; **71,** middle leg; **72,** hind leg; **73,** hind tibia; **74,** mesosomal dorsum.

side (Fig. 78), where *B. standleyi* has 3 (Fig. 63). The apical process of the hind tibia is bidentate (Fig. 81) instead of tridentate as in *B. standleyi, B. mariae,* and *B. carlosi. Male:* The smallest described as new. The anterior side of the mesosomal dorsum is quite narrow in relation to the rest of the structure (Fig. 89). The hind tibia has 3 large and 2 small apical teeth (Fig. 88).

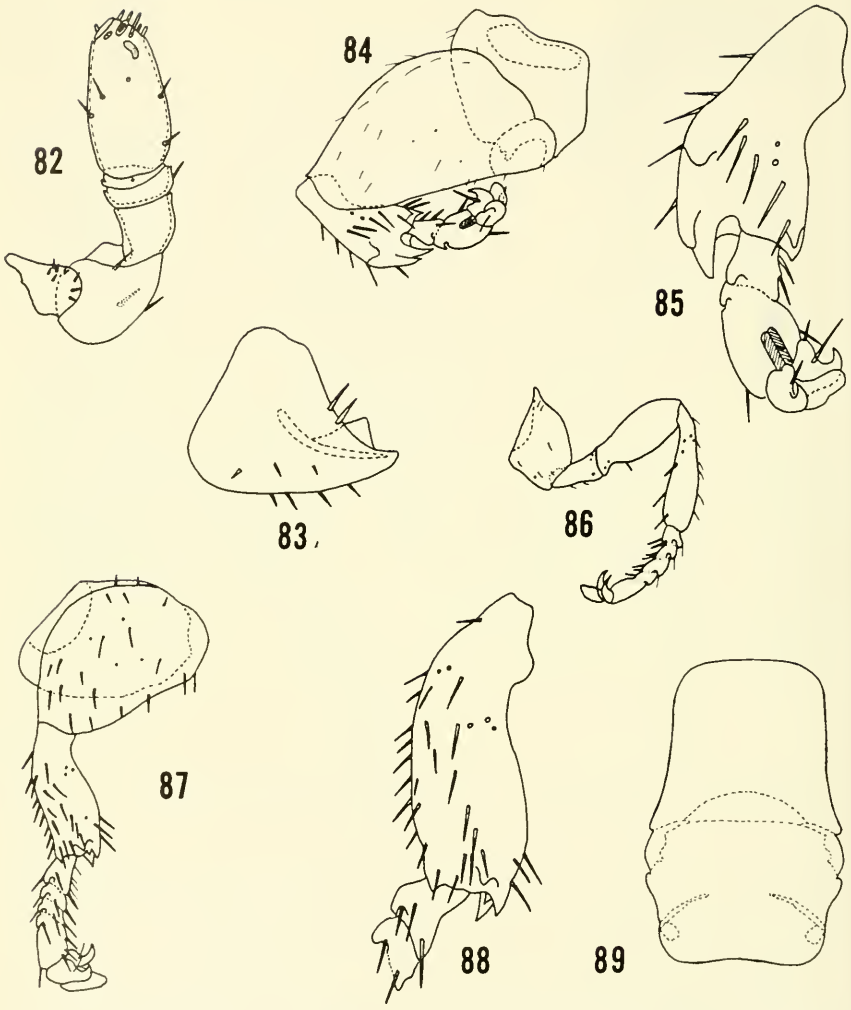
Types: Holotype female, specimen No. 1 (slides 1339-1340-1341). Female paratypes: No. 2 (848), No. 3 (1037-1038), No. 4 (1331), No. 5 (1332). Allotype male, No. 6 (846-847). Male paratypes: No. 7 (840-841), No. 8



FIGS. **75-81.** *Blastophaga orozcoi. Female:* **75,** antenna; **76,** maxillo-labial complex; **77,** front leg; **78,** front tibia; **79,** middle leg; **80,** hind leg; **81,** hind tibia.

(842-843), No. 9 (844-845), No. 10 (1042). *Host: F. colubrinae* Stand. *Locality:* Puerto Viejo, Heredia, Costa Rica. *Date:* May 16, 1964. Many other specimens of both sexes are preserved in vial No. 13.

Female: (1) Body length 0.94 mm; ovipositor length 0.38 mm. (2) Head and dorsum of body blackish amber. (3) Scape honey colored, rest of antenna blackish. (4) Body blackish with venter honey colored. (5) Front and hind femora blackish, rest of legs honey colored. (6) Head subtriangular, much wider than long, posterior side straight. (7) Compound eye much longer than gena. (8) Premandibular projection with 2 bristles; clypeus with 10 setae; epistomal margin rounded, submedial lobes very wide but not prominent, medial lobe wide and slightly prominent. (9) Antenna (Fig. 75) with scape suboval, length less than twice width; flagellomere 1 with apical process surpassing apex of 2; 2 slightly longer than wide; 3 to 8 with longitudinal sensilla; 3 wider than long, with 4 sensilla; 4 slightly wider than long, with 6 or 7 sensilla; 5 wider than long, with 6 or 7 sensilla; 6 and 7 with same dimensions as 5, each with 6 sensilla; 8 narrower than 7, with 6



FIGS. 82-89. *Blastophaga orozcoi*. *Male:* 82, antenna; 83, mandible; 84, front leg; 85, front tibia; 86, middle leg; 87, hind leg; 88, hind tibia; 89, mesosomal dorsum.

sensilla; 9 subconical, longer than wide, with 3 or 4 longitudinal and 2 circular sensilla. (10) Mandible (Fig. 120) bidentate, as long as wide, with 7 or 8 ventral ridges. (11) Mandibular appendage with 7 or 8 lamellae. (12) Maxilla (Fig. 76) with 1 medial and 1 subapical bristle. (13) Labium (Fig. 76) with 1 apical bristle. (14) Front leg (Fig. 77): coxa with corbicula, coxal length more than twice width; femoral length more than 3 × width; tibial length twice width, tibia with 2 apical teeth located anteriorly and 1 posteriorly (Fig. 78); tarsus with segment 1 longer than 2, shorter than 5; 3 and 4 of

equal length, 5 longest. (15) Middle leg (Fig. 79): coxal width almost twice length; femoral length 4 × width; tibial length 6 × width; tarsus with segment 1 slightly longer than 5; 2 and 3 of equal length but shorter than 1; 4 shorter than 3. (16) Hind leg (Fig. 80): coxal length less than twice width; femoral length twice width; tibial length 3 × width, apical process bidentate (Fig. 81); tarsus with segment 1 much longer than 5; 2 and 3 of equal length and shorter than 1; 4 slightly shorter than 3. (17) Front wing length slightly more than twice width, humeral vein with 2 pustules (some specimens with 3), marginal vein shorter than stigmal, stigmal with 2 pustules (some specimens with 3 or 4), postmarginal atrophied. (18) Hind wing length 5 × width. (19) Mesosternum: sternal corbiculae with 5 hairs in anterior row and 2 located posteriorly; sternum with 4 or 5 hairs on each side.

Male: (20) Head as wide as long. (21) Antenna as in Figure 82. (22) Maxillo-labial complex lobiform with 3 apical small lobelets, middle one with 1 apical and 2 basal bristles, main structure with 2 medial bristles. Mandible as in Figure 83. (23) Front leg (Fig. 84): coxa as wide as long; femoral length less than twice width; tibial length more than twice width, 5 apical teeth (Fig. 85); tarsal segment 1 shorter than 2. (24) Middle leg (Fig. 86): coxa as wide as long; femoral length slightly less than twice width; tibial length 4 × width; tarsus as long as tibia, segment 1 longer than 2; 2 and 3 of equal length, 4 shortest, 5 longest. (25) Hind leg (Fig. 87): coxa longer than wide; femur wider than coxa; tibia with 5 apical teeth (Fig. 88); tarsus as long as tibia, segment 1 shorter than 5; 2, 3, and 4 decreasing progressively in length, 5 longest. (26) Mesosomal dorsum (Fig. 89) with length 0.60 mm, maximum width 0.31 mm, anterior width 0.30 mm, posterior width 0.27 mm.

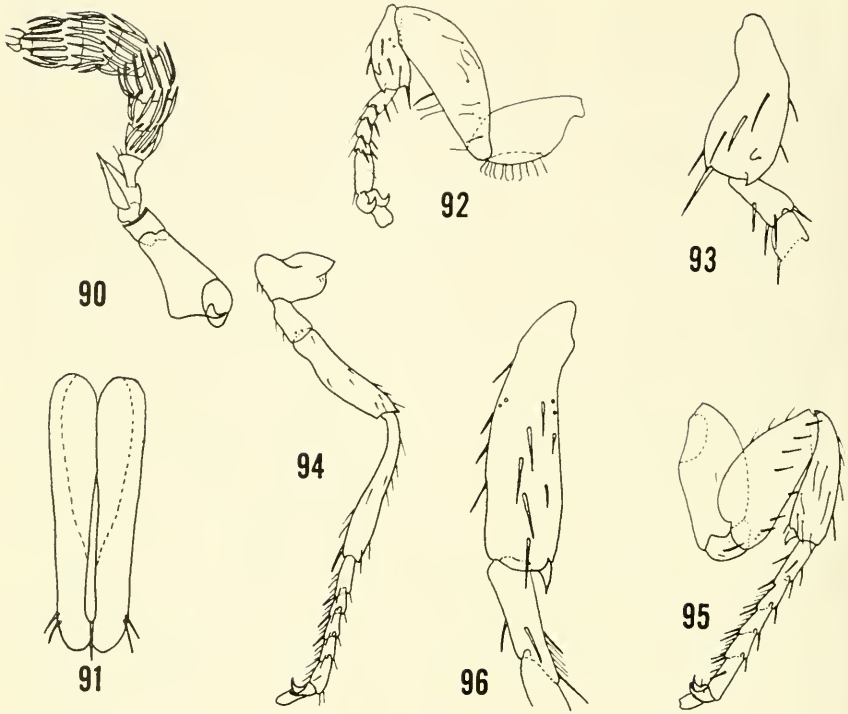
This species is named for my Costa Rican friend, Professor José María Orozco Cazorla, of the Ministerio de Agricultura y Ganadería, San José.

Blastophaga ileanae new species

(Figs. 90-96, 121)

Comparative comments: *Female:* This is the smallest wasp newly described (length less than 1.00 mm). The antenna has a very small last flagellomere (Fig. 90), less conspicuous than in the other species described. The maxilla possesses no medial bristles although it has 2 subapical ones, as in *B. cumanensis.* The labium has a single apical bristle (*B. cumanensis* has 2). The front tibia has 2 apical teeth on the anterodorsal side (Fig. 93) as in *B. orozcoi* (Fig. 78) but it differs from that and all the other new species described because its hind coxa has only 1 apical tooth (Fig. 96). *Male:* Unknown.

Types: Holotype female, specimen no. 1 (slides 1047-1048). Female paratypes: No. 2 (830-831), No. 3 (832), No. 4 (833-834-835), No. 5 (836).



FIGS. 90-96. *Blastophaga ileanae*. *Female:* 90, antenna; 91, maxillo-labial complex; 92, front leg; 93, front tibia; 94, middle leg; 95, hind leg; 96, hind tibia.

Host: F. schippii Stand. *Locality:* Puerto Viejo, Heredia, Costa Rica. *Date:* May 16, 1964.

Female: (1) Body length less than 1.00 mm. (2) Head and body blackish; (3), (4), and (5) unknown. (6) Head subtriangular, wider than long, posterior side slightly concave. (7) Compound eye longer than gena. (8) Premandibular projection without bristles; clypeus with 2 setae; epistomal margin with wide but not prominent submedial lobes, medial lobe acute and prominent. (9) Antenna (Fig. 90) with scape subtriangular, almost twice as long as wide, flagellomere 1 with apical process reaching apex of 2; 2 slightly longer than wide; 3 to 8 with longitudinal sensilla; 3 slightly longer than wide, with 5 or 6 sensilla; 4 as long as wide, with 6 sensilla; 5 and 6 subequal, wider than long, each with 7 sensilla; 7 to 9 forming a loose club; 7 wider than long, with 7 sensilla; 8 longer than wide, with 6 sensilla; 9 subconical, very small, apparently fused to 8, without sensilla. (10) Mandible (Fig. 121) bidentate (apparently unidentate), wider than long, with 5 or 6 ventral ridges. (11) Mandibular appendage with 6 lamellae (some specimens 7). (12) Maxilla (Fig. 91) with no medial and 2 subapical

bristles. (13) Labium (Fig. 91) with one apical bristle. (14) Front leg (Fig. 92): coxa with corbicula, coxal length twice width; femoral length 3 × width; tibial length twice width, 2 apical teeth located anteriorly and 1 very small one posteriorly (Fig. 93); tarsus with segment 1 longer than 2; 2 as long as 3; 4 shorter than 3, 5 longest. (15) Middle leg (Fig. 94): coxa much wider than long; femoral length 4 × width; tibial length 6 × width; tarsus with segment 1 as long as 5, segments 2 and 3 of equal length, 4 shortest. (16) Hind leg (Fig. 95): coxal length twice width; femoral length twice width; tibial length 2.7 × width, apical process unidentate (Fig. 96); tarsus with segment 1 longer than 5; 2 slightly longer than 3; 3 and 4 of equal length. (17) and (18) unknown. (19) Mesosternum: sternal corbiculae with 5 hairs in anterior row and 3 to 5 located posteriorly, sternum with 4 hairs on each symmetrical side.

(20) *Male:* Unknown.

This species is named for my daughter, Ileana María Ramírez L.

Comparative Comments on Neotropical Agaonidae and Their Hosts

This part consists of information on previously described neotropical agaonids, principally those now known to occur in Costa Rica, including some remarks on their hosts. Table 4 summarizes measurements and figures to show mandibles of females of these as well as the new species.

All the previously known agaonids studied in connection with this work were described by Guido Grandi (1919, 1920, 1925, 1934, 1938, 1952, and 1963b). Collection data for all species are those of the hosts as shown in Table 1.

Table 2. Sizes in mm of body, ovipositor and mandible of agaonid females described.

Blastophaga	Body length	Ovipositor length	Mandible length
B. cumanensis	2.10	1.00	0.27-0.30
B. mariae	1.70	1.02	0.25-0.29
B. carlosi	1.67	1.09	0.21-0.27
B. urbanae	1.33	0.68	0.16-0.20
B. standleyi	1.03	0.56	0.15-0.16
B. orozcoi	0.94	0.38	0.12-0.14
B. ileanae			0.10-0.11

Table 3. Dimensions in mm of mesosomal dorsum of agaonid males described.

	Length	Maximum width	Anterior width	Posterior width
B. cumanensis	1.40	0.74	0.45	0.48
B. mariae	1.20	0.72	0.60	0.45
B. carlosi	1.17	0.72	0.60	0.48
B. urbanae	0.90	0.49	0.36	0.33
B. standleyi	0.78	0.40	0.30	0.27
B. orozcoi	0.60	0.31	0.30	0.27

TABLE 4. Maximum, Minimum, and Average lengths in mm of the Mandibles of Females of 17 New World *Blastophaga*.

Blastophaga sp.	Minimum	Maximum	Average	Fig. No.
B. hoffmeyeri Grandi	0.300	0.325	0.324	105
B. cumanensis new sp.	0.288	0.325	0.297	106
B. mariae new sp.	0.250	0.288	0.270	107
B. torresi Grandi	0.225	0.288	0.257	108
B. astoma Grandi	0.238	0.263	0.256	109
B. amabilis Grandi	0.225	0.255	0.244	110
B. aguilari Grandi	0.225	0.250	0.235	111
B. carlosi new sp.	0.213	0.269	0.235	112
B. baschierii Grandi	0.200	0.250	0.229	113
B. estherae Grandi	0.213	0.238	0.226	114
B. tonduzi Grandi	0.183	0.220	0.198	115
B. urbanae new sp.	0.163	0.200	0.183	116
B. aemula Grandi	0.175	0.177	0.176	117
B. jimenezi Grandi	0.163	0.180	0.172	118
B. standleyi new sp.	0.150	0.162	0.155	119
B. orozcoi new sp.	0.119	0.137	0.130	120
B. ileanae new sp.	0.100	0.113	0.104	121

Blastophaga astoma has been placed in the subgenus *Tristaniella*. The female has the postmarginal vein in the front wing. Its mandibular appendage (Fig. 109) usually has 5 lamellae (some specimens only 4); other species studied have 6 or more. The maxilla possesses 1 medial and 2 subapical bristles. This is the only known agaonid in which the male is astomous.

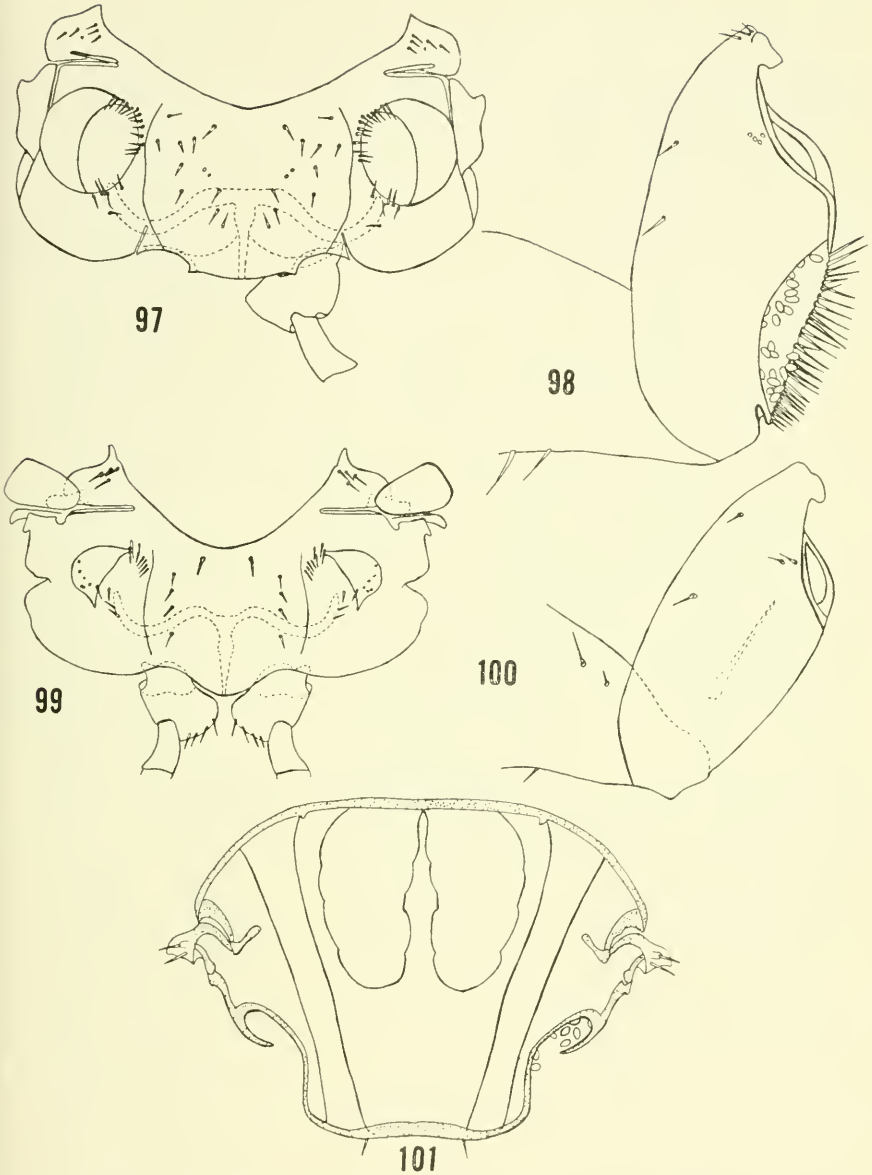
Host: *B. astoma* is the pollinator of *Ficus (Urostigma) torresiana*. Grandi (1920) reports that this species was collected in the receptacles of *Ficus (Pharmacosycea) crassiuscula* in Costa Rica, but this must certainly have been an error.

Blastophaga aguilari, B. baschierii, B. bruneri, and *B. torresi* have been placed in the subgenus *Julianella* because the humeral vein in the front wing is incomplete and the costal cell is open. Although these characters are variable and not correlated with others, the species are discussed in a group below.

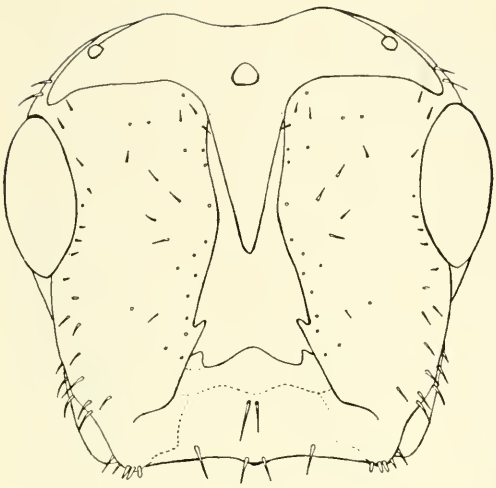
Blastophaga baschierii differs from the other three because its humeral vein ends in a distinctive clavola (Grandi, 1952, p. 52). The maxilla has 3 medial and 2 subapical bristles. The mandibular appendage possesses 7 or 8 lamellae (Fig. 113).

Host: Grandi (1952 and 1963a) does not report the host of *B. baschierii* and mentions as locality, Cuernavaca, Morelos, México. I have found this species pollinating and developing in the receptacles of *F. turbinata* in Venezuela and Panamá.

The females of *B. aguilari* are quite similar to *B. baschierii,* having similar chaetotaxy of the labium and maxilla, but the female of *B. baschierii* can be distinguished particularly because of the length of the fourth antennal seg-



Figs. 97-101. Corbiculae of *Blastophaga*. 97, mesosternum of *B. cumanensis* showing sternal corbiculae (ventral view); 98, front coxa of *B. cumanensis* showing the coxal corbicula (ventral view); 99, mesosternum of *B. carlosi* showing sternal corbiculae (ventral view); 100, front coxa of *B. carlosi* without corbicula (ventral view); 101, cross section of mesothorax of *B. jimenezi* showing position and shape of sternal corbiculae (pollen grains in place on right side).



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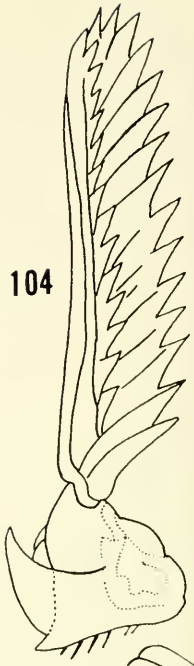

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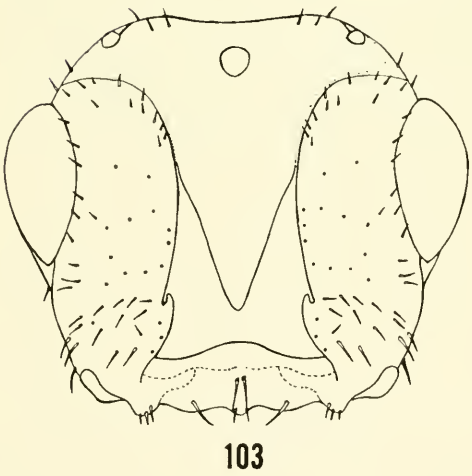

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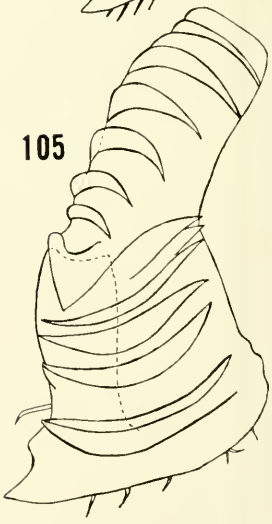


105

FIGS. **102-105.** **102,** head of *Blastophaga mariae;* **103,** head of *B. carlosi;* **104,** mandible of *Tetrapus costaricanus;* **105,** mandible of *B. hoffmeyeri.*

ment and the characteristic clavola and chaetotaxy of the front wing (Grandi, 1952). The mandibular appendage in *B. aguilari* has 7 or 8 lamellae (Fig. 111).

Host: I have found *B. aguilari* pollinating and developing in the receptacles of *F. lapathifolia* in Costa Rica, as Grandi (1919) reports.

Blastophaga torresi females differ from the other three species that have been listed in *Julianella* because its maxilla has 4 medial bristles (3 or 2 in the others). Its mandibular appendage has 7 or 8 lamellae (Fig. 108).

Host: This wasp is the pollinator of *F. velutina* as Grandi (1920) reports.

Blastophaga bruneri females differ from the other species listed in *Julianella* because its maxilla has only 2 medial bristles (other species have 3 or 4). Its mandibular appendage possesses 6 lamellae (some specimens 7) (Fig. 6 of Grandi, 1934).

Host: Grandi (1934) reports this species from receptacles of *F. coombsii* in Puerto Padre, Provincia de Oriente, Cuba. I found *B. bruneri* in the receptacles of a *Urostigma* species on San Andrés Island, Colombia. This fig was apparently also *F. coombsii*.

The other known *Blastophaga* studied are characterized by the humeral vein of the front wing reaching the edge of the wing, closing the costal cell, and by the presence of a stigmal vein.

B. jimenezi is easy to separate from the other species because its mandible possesses a very long apical tooth, so that it appears monodentate (Fig. 118). The only other New World *Blastophaga* known to me that possesses a similar mandible is the pollinator of *F. aurea* in Florida (not included here). The mandibular appendage of *B. jimenezi* usually has 6 lamellae (some specimens have 7 or 8) (Fig. 118).

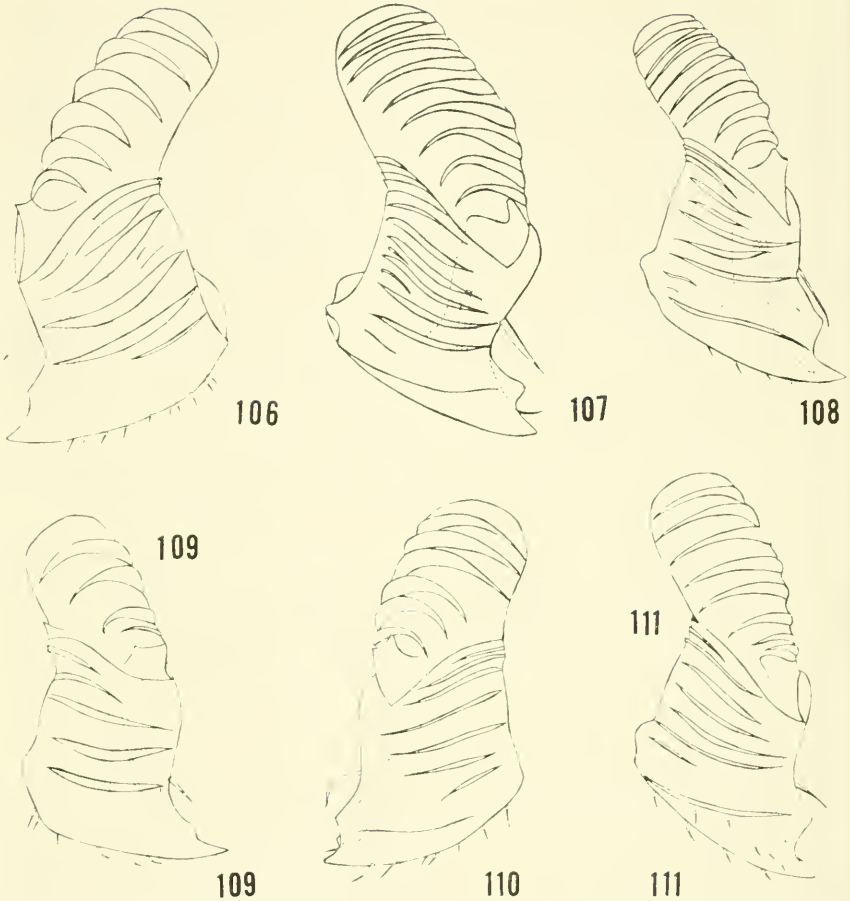
Host: *F. jimenezii* as Grandi (1919) reports.

Blastophaga estherae is easy to distinguish from the other species studied because the apical process of the hind tibia of the female is annular, and with a series of large and small teeth (Grandi, 1919, Fig. IV). The only species studied which possesses a similar hind tibia is *B. urbanae* (Fig. 51), but *B. urbanae* differs from *B. estherae* by the flat projecting bristles on the last 7 flagellomeres (Fig. 45). The mandibular appendage of *B. estherae* has 10 lamellae (Fig. 114) (Grandi, 1919, Fig. IV).

Host: *B. estherae* develops in the receptacles of *F. costaricana* in Costa Rica as Grandi (1919) reports. In some supposed *F. costaricana* I have found another undescribed species of *Blastophaga*.

Blastophaga tonduzi is easy to distinguish from the other species studied because the front tibia of the female has 2 apical teeth located anteriorly (Grandi, 1919, Fig. X). In this respect this wasp resembles *B. amabilis*, but they differ especially in the chaetotaxy of the maxilla; *B. tonduzi* has no medial bristles, while *B. amabilis* has 1 medial bristle. The mandibular appendage in *B. tonduzi* has 6 or 7 lamellae (Fig. 115).

Host: *B. tonduzi* develops in Costa Rica and in Venezuela in the receptacles of *F. hemsleyana*, as Grandi (1919) reports.

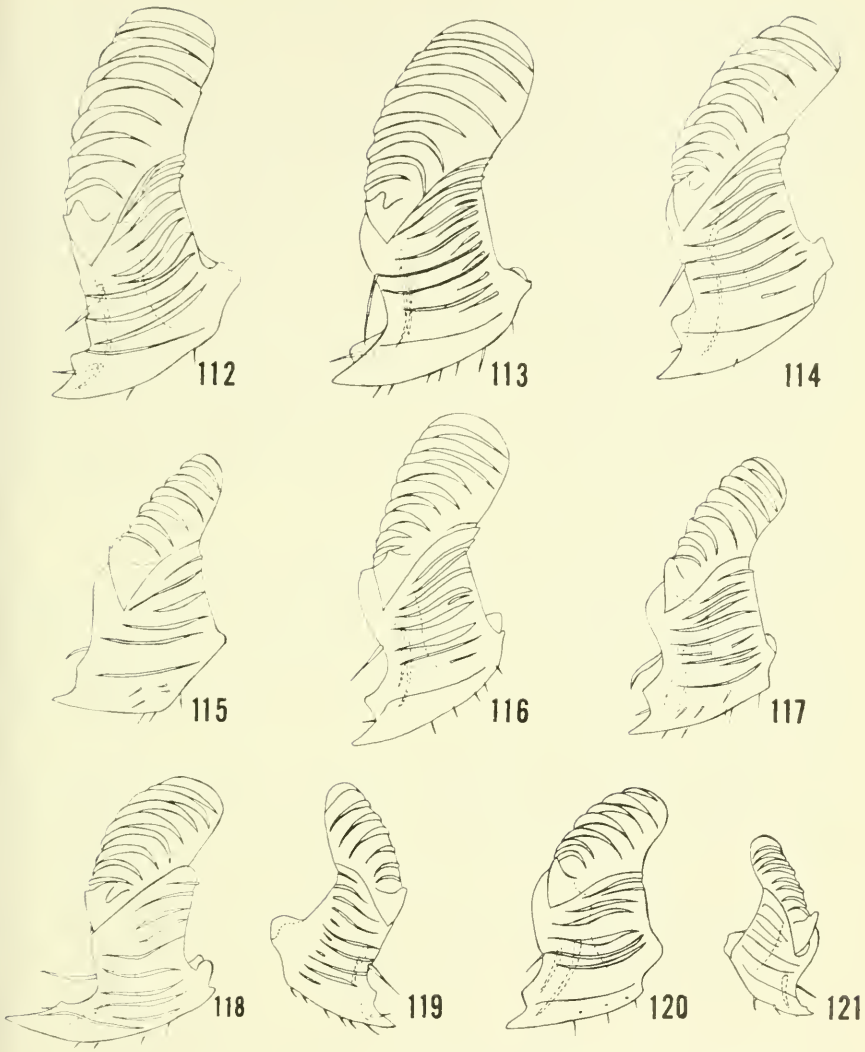


FIGS. 106-111. Mandibles of females. 106, *Blastophaga cumanensis;* 107, *B. mariae;* 108, *B. torreri;* 109, *B. astoma;* 110, *B. amabilis;* 111, *B. aguilari.*

Blastophaga hoffmeyeri is the largest among the species studied and also possesses the largest mandible (Fig. 105). The female can be distinguished from the other known New World *Blastophaga* because of its subquadrangular scape (Grandi, 1934, Fig. IV) and its apparently tridentate mandible (Fig. 105). The mandibular appendage has 6 or 7 lamellae.

Host: I have found this wasp always developing in the receptacles of *F. obtusifolia* in Costa Rica and Panamá. Grandi (1934) described this species from Paraguay from an unknown fig.

B. aemula can be distinguished from other *Blastophaga* because of the chaetotaxy of the female labium, which has a single apical bristle. This is the only wasp of the group studied which possesses 3 apical teeth on the



FIGS. 112-121. Mandibles of females. 112, *Blastophaga carlosi;* 113, *B. baschierii;* 114, *B. estherae;* 115, *B. tonduzi;* 116, *B. urbanae;* 117, *B. aemula;* 118, *B. jimenezi;* 119, *B. standleyi;* 120, *B. orozcoi;* 121, *B. ileanae*.

anterodorsal side of the front tibia combined with the labial chaetotaxy described. Its mandibular appendage has 8 lamellae (Fig. 117).

Host: If the identification of the wasp is correct, *B. aemula* develops in the receptacles of *F. trachelosyce* in Costa Rica. The specimens agree with Grandi's excellent drawings and description but Grandi (1938) reports this species from *F. luschnatiana* in Brazil, while stating that the identification

of the fig is not perfectly certain. DeWolf (1960) says that *F. trachelosyce* is found in Panamá and Colombia and probably in southwestern Costa Rica, but not Brazil.

Female *Blastophaga* found pollinating the receptacles of *F. nymphaeaefolia* are quite similar to *B. amabilis* but I am not sure about the identity of this wasp because I do not have males for comparison and because the labium of the specimens I have collected in Costa Rica possesses only one bristle instead of 2 as reported by Grandi (1938) for this wasp in Brazil. The mandibular appendage of females observed (Fig. 110) has 6 lamellae. Grandi (1938) reports the presence of 7 lamellae.

Host: DeWolf (1960) reports that *F. nymphaeaefolia* is found from Panamá to the mouth of the Amazon; thus the possibility exists that *B. amabilis* develops in Brazil also in the receptacles of the same fig.

Tetrapus costaricanus: The females possess mandibles with a very long, saw-like proximal process (Fig. 104) as in the majority of *Tetrapus* females, and the males are tetrapous.

Host: This wasp develops in the receptacles of *F. glabrata* in Costa Rica and Panamá. Grandi (1925, 1963a) does not report the host.

The pollinator of *Ficus crassiuscula* in Costa Rica is the most peculiar wasp of the genus *Tetrapus*. It will soon be described as a new species. The mandible of the female has 2 saw-like mandibular appendages, while the other known species possess only one. The males have three functional pairs of legs.

As shown above there are several discrepancies between the hosts of wasps studied and the reports of Grandi (1963a). Furthermore there are differences between the way DeWolf (1960, 1967) classifies some of the New World figs and the manner the agaonids use some of his species as biological units. The most important discrepancy is that *Blastophaga astoma* is the pollinator of *F. (Urostigma) torresiana* and not of *F. (Pharmacosycea) crassiuscula* as Grandi (1920) reported. DeWolf (1967) considers *F. (Urostigma) torresiana* to be a synonym of *F. (Pharmacosycea) macbridei.*

B. jimenezi is the specific pollinator of *Ficus jimenezii* as Grandi (1919) reports. DeWolf (1960) considers that *F. jimenezii, F. isophlebia,* and *F. tuerckheimii* are one species *(F. tuerckheimii).* I have found that *F. isophlebia* is the host of *B. urbanae, F. tuerckheimii* of both *B. mariae* and *B. carlosi.* Standley (1917) mentions these three species of figs from Costa Rica and considered them close relatives. These figs are found in Costa Rica growing in different zones and altitudes. *F. tuerckheimii* thrives above 1500 m, *F. jimenezii* is very common in the Central Valley and in the Pacific Zone at altitudes from approximately 800 m to 1500 m and *F. isophlebia* is found in dry lowlands of Guanacaste. *F. isophlebia* was described by Standley (1917) from David, Chiriquí, Panamá at altitudes from 30 to 80 m.

That *F. jimenezii* and *F. tuerckheimii* are possibly related species is revealed by the presence of a hybrid between the two at El Roble, Heredia, Costa Rica, where their ranges meet. This is the only hybrid I have found among New World figs. The young figs of this hybrid were entered by *B. jimenezi* (the pollinator of *F. jimenezii*) and by *B. mariae* and *B. carlosi* (the pollinators of *F. tuerckheimii*) but when the figs became ripe, reaching the size of ripe figs of *F. jimenezii*, only *B. jimenezi* appeared. *B. mariae* and *B. carlosi* did not develop.

B. estherae was found to use as host *F. costaricana*, as Grandi (1919) reports, but in some supposed *F. costaricana* trees I have found a different species of *Blastophaga*, not described. Two possibilities could explain the presence of two species of *Blastophaga* in this species. *F. costaricana* could be pollinated by two species of wasps as is *F. tuerckheimii*, or there may be in the Central Valley of Costa Rica a sibling complex of figs whose species can be recognized by the pollinators.

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DISTRIBUTION AND ZOOGEOGRAPHY OF PERUVIAN BATS, WITH COMMENTS ON NATURAL HISTORY

By

Merlin D. Tuttle

Vol. XLIX Pages 45-86 Oct. 29, 1970 No. 2

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Vol. XLIX Pages 45-86 Oct. 29, 1970 No. 2

Distribution and Zoogeography of Peruvian Bats, with Comments on Natural History

Merlin D. Tuttle

ABSTRACT

Biological data are presented for 54 species of bats collected in 1963 and 1964, and zoogeographic problems are discussed. A list of Peruvian bats, based on specimens examined and those reported in the literature, is presented. Previously unreported specimens contained in the collections of the American Museum of Natural History, the Field Museum of Natural History, and the United States National Museum are included. Some erroneous records are clarified. Five genera and 16 species of bats are reported from Perú for the first time.

INTRODUCTION

Owing to its strikingly diverse physiography, Perú is inhabited by an unusually rich and somewhat peculiar chiropteran fauna. The purpose of this paper is to summarize the current state of knowledge concerning the distribution and biology of the 105 species of bats known from that country. Due to the paucity of information available, it may be assumed that future collecting will reveal the presence of many additional species. Since Tschudi's 1844 work on the fauna of Perú, there have been only a few contributors to knowledge of Peruvian bats. Aellen (1965) reported on a collection from northwestern Perú containing 27 specimens of seven species; Sanborn (1932*a* and elsewhere) and Thomas (1893 and elsewhere) reported mostly on small local collections from the Amazon region. The only monographic study of Peruvian bats (de la Puente, 1951) was geographically restricted to the area near Lima on the west coast. Most of the earlier collections of bats were made by natives hired to make general collections of mammals. Modern collecting techniques such as the use of mist nets were then unknown. Thus, it must be assumed that many species have escaped notice, even in the areas where collecting has been most intense.

In the course of extensive field investigations sponsored by Andrews University in 1964, more than 1300 bats were collected in central Perú. Among these were three genera and 13 species previously unreported from the country. Other bats, known previously from one or two Peruvian localities, were found to be more widely distributed within the country. In evaluating these records, I have perused literature pertaining to Perú and have examined specimens, some unreported, in several North American collections.

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METHODS AND MATERIALS

This paper is based principally upon collections made in central Perú by me in June, 1963, by members of the Andrews University Department of Biology working with me in June and July, 1964, and by my brother, Arden L. Tuttle, in August, 1964. In addition, specimens were examined in the collections of the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), and United States National Museum (USNM).

Reproductive and other biological data, even for the most common of Peruvian bats, are few. For this reason, I have included as much information as possible on habitats and reproduction; all such data were obtained by personal observation or by other members of our field party.

All measurements are given in millimeters and weights are in grams. Measurements of the forearm represent the longest measurable distance between the wrist and the elbow with wing fully flexed and dry. Crown-rump length of embryos was measured from the crown to the most distant point on the rump as the embryo normally rests within the uterine sac, and

includes the sac. All pregnant females had but a single embryo unless otherwise noted. No attempt was made to measure more than a sample of the embryos or testes of common species. Both the length (given first) and the width of the testes were measured, and are not recorded for juveniles. Considerable individual variation, the significance of which is not known, will be noted with respect to measurements of testes of adult males.

South American maps often disagree concerning boundaries and spellings of place-names. Consequently, all boundary lines and names of localities are given according to the "Map of Hispanic America" (published by the American Geographical Society), excepting boundaries for the Departamento de Pasco, which did not exist until 27 November 1944 when northern Junín and southern Huánuco were joined to form a new department. In some instances it was advisable to correct slight misspellings (indicated by brackets). Unfortunately, the names of provinces and departments (see Fig. 1) seldom have been included in locality records. Most authors have, however, mentioned larger towns and rivers in conjunction with collection sites, thus making its possible to determine provincial and departmental designations with minimal error. Locality names not included on the "Map of Hispanic America" series (and the accompanying gazetteer, "Geographical names in Ecuador and Peru," 1944), published by the American Geographical Society, are indicated by an asterisk. When it was impossible to substantiate the exact location of an important distributional record, an appropriate explanation is included.

The reported distribution of each species of bat known to inhabit Perú is given (from the northernmost locality to the southernmost) and substantiated by literature citations or museum specimens. Only marginal records are given for common species. Until revisionary works now in progress are completed, or until additional specimens are available, the classification, especially at the infraspecific level, of several species will remain in question. For this reason, I have used only specific names although I have made mention, where appropriate, of subspecific names that have been used with reference to Perú. Nomenclature follows Cabrera (1958) unless a more recent work is cited.

Specimens that my colleagues and I collected in 1963 and 1964 are deposited in the American Museum of Natural History unless otherwise indicated. A brief description of sites at which collections were made in those two years follows the accounts of species.

FIG. 1. Map of Perú indicating department boundaries and major river systems. Departments are numbered as follows: 1, Tumbes; 2, Amazonas; 3, Loreto; 4, Piura; 5, Cajamarca; 6, Lambayeque; 7, San Martín; 8, La Libertad; 9, Ancash; 10, Huánuco; 11, Lima; 12, Callao; 13, Pasco; 14, Junín; 15, Huancavelica; 16, Ayacucho; 17, Cuzco; 18, Madre de Dios; 19, Ica; 20, Apurímac; 21, Puno; 22, Arequipa; 23, Moquegua; 24, Tacna. Rivers are labeled as follows: A, Marañón; B, Amazonas; C, Huallaga; D, Ucayali.

ENVIRONMENT OF PERU

Geological History

The Andes have been of prime importance in determining the climate and distribution of life in Perú. An Andean uplift of between 5000 and 10,000 feet is thought to have occurred during Tertiary time, followed by an additional uplift of 200 to 1200 feet in the Quaternary (Bosworth, 1922:157; Garner, 1959). Prior to the first uplift, southern Perú apparently underwent a long period of erosion in the east, whereas parts of the west were covered with great lava sheets. In central and northern Perú, a relatively moist climate probably supported mesophytic vegetation until the Andean uplift imposed an arid climate and accompanying zerophytic plant life on the coastal region (Ogilvie, 1922:13, 109).

Pleistocene glaciation was widespread in the Peruvian Andes (McLaughlin, 1924; Douglas, 1933:315-316) and, according to Bowman (1916:214), "some of the glaciers were over a thousand feet thick; a few were nearly two thousand feet thick, and the cirques that fed them held snow and ice at least a half mile deep." Bowman suggested that, in many places in eastern Perú, glaciers 5-10 miles long may have extended nearly to the tree line at elevations of about 10,000 feet. On the southwestern slope of the Andes, Fenner (1948) reported that some glaciers may have descended to 12,800 feet and possibly in rare instances to 10,980 feet, but that 14,000 feet was the common lower limit. In the central Peruvian Andes, Harrison (1943) found evidence that glaciers had descended to about 13,500 feet on the western side and to less than 12,000 feet on the eastern side. Morains and other deposits have been interpreted to indicate three distinct stages of Pleistocene glaciation (McLaughlin, 1924).

Clastic material deposited in Andean valleys indicates that the Pleistocene climate was one of alternating periods of aridity and humidity both to the east and west of the mountains, but aridity and deposition apparently dominated in the west, and humidity and incision in the east (Garner, 1959). Extensive erosion cut steep, cliff-walled canyons and gorges, as much as 7000 feet deep (Johnson and Platt, 1930:26), especially on the eastern slope where precipitation was heaviest (Ogilvie, 1922:14). At the base of the Andes, enormous alluvial fans partly filled the valleys (Bowman, 1916:70) and spread outward onto the plains.

The coastal plain or "littoral" region of northwestern Perú forms a desert 10-20 miles wide between the Pacific Ocean and the Andes. A great submarine fault-scarp marks a main fracture along the coast; it has been suggested that at this fracture the "littoral" has been lowered and raised repeatedly during the Quaternary. The overall trend, however, was a gradual process of uplift (Bosworth, 1922:194-196). The littoral region is

rugged and much dissected, although elevations usually are well below 1000 feet. Large areas of tablelands, known as "tablazos," consist of thin sheets of Quaternary marine sediments lying horizontally over upturned Tertiary rocks. The "tablazos" cover most of the littoral zone from the mountains to the sea.

It is clear that the littoral region was better watered at times during the Pleistocene than at present. Lemon and Churcher (1961) noted that "the vertebrate fauna found in the tar seep deposits [at Talara] include many forms characteristic of a habitat considerably wetter than any found in the area at the present day. Although it is not possible to say that the whole region was well watered during Pleistocene times, there must have been numerous permanent or semi-permanent streams." This also is indicated by an abundance of vegetable material in the tar seeps and by the deep river valleys that have been cut into the elevated marine terraces. The local coastal climate probably differed little from that of the present (Lemon and Churcher, 1961). Thus, it must be assumed that runoff from the high Andes was much greater in the Pleistocene than now.

East of the Andes much of the geological record is buried beneath enormous alluvial deposits and the dense jungle vegetation of Amazonas, and little precise information is available for this region.

Climate

Perú is roughly divisible into three climatic regions: Pacific coastal, high Andean, and Amazonian. These are characterized by desert, semidesert, and tropical rainforest climates, respectively. Winter comes in June or July, and the rainy season is approximately from November to March. There is about a 10-degree decrease in mean annual temperature from north to south due to latitude (Ogilvie, 1922:28).

The Pacific coastal plain is characterized by a sudden change from excessive to scanty rainfall. The north side of the Gulf of Guayaquil receives 1000 mm of rain annually, whereas Tumbes on the south side receives only about 250 mm (Kendrew, 1953:478). Farther south, rain falls rarely and the only moisture, other than that from widely scattered rivers, comes to the coastal hills or "lomas" and is derived from fog banks that are prevalent in winter. Between the coastal hills and the Andes lies an extensive belt of essentially moistureless desert where the only notable life is restricted to river valleys.

The highland climate is characterized by low precipitation, a great daily range of temperature, and a high percentage of clear days, promoting rapid heating by day and cooling by night (Ogilvie, 1922:16). Whereas precipitation occurs almost daily in the highest parts of the northern Andes, it decreases rapidly toward the south (Ogilvie, 1922:28).

Most of the precipitation east of the Andes is derived ultimately from the Atlantic Ocean. Excessive rainfall there is due to the orographic influence of the Andes upon trade winds as they are forced up the eastern slopes (Kendrew, 1953:479). The belt of maximum precipitation lies between 4000 and 10,000 feet (Bowman, 1916:147), but rainfall is heavy throughout the whole Amazonas region. Tingo Maria, in the central Amazonas, receives an annual mean rainfall of 3192.6 mm (World weather records, 1966:150).

Physiography and Vegetation

Ecologically, Perú is one of the most diverse and complicated countries of the world. It comprises approximately 1,285,215 square kilometers in which Tosi (1960) has mapped the geographic distribution of 35 different vegetative formations.

The Andean Cordillera forms the backbone of Perú and divides the country into three general regions: (1) desert coast and piedmont on the west, an arid strip 10-100 miles wide; (2) the sierra, a series of high mountain chains with their peaks, plateaus, and valleys; and (3) the montaña, which is the hot, humid, low country east and northeast of the Andes, consisting of foothills and true Amazonian lowland.

A further division into six general physiographic regions has been described by Ogilvie (1922:29) as follows: (1) coastal hills with moisture and vegetation in winter; (2) desert piedmont with oases in some of the valleys; (3) the Puna (high, dry, unforested cordillera with intermontane basins in the south); (4) the Altiplano with moisture and forest; (5) broken mountain slopes (moist and forested); and (6) plains (hot, moist, and mostly forested).

The Pacific seaboard is largely desert where, for long stretches between valleys, there is little evidence of life and no water (Ogilvie, 1922:20). In the north (north of Chiclayo), runoff from the Andes and frequent fog permit the growth of dry forest along the western slopes, and in the southeastern section of Departamento de Tumbes there is even a small area of humid forest. South of Chiclayo the dry forest quickly narrows, and beyond Trujillo the forest is broken and confined to widely separated river valleys (Tosi, 1960: maps 1-2). For the most part, southwestern Perú forms one of the world's most extreme deserts. The natural vegetation of the river valleys "includes trees—the *chanar (Gourleja decorticans),* the *molle* or pepper *(Schinus molle),* and a willow *(Salix Humboldtiana)*—as well as a number of shrubs" (Ogilvie, 1922:112).

On the western slopes of the Andes the piedmont desert gradually gives way to the semidesert, treeless grassland that is typical of most of the high Andes. The high grassland between the Cordillera Occidental and the Cordillera Oriental, the eastern slope of which overlooks the Amazonian

plains, is known as the "Puna" (Ogilvie, 1922:115). Summer and winter bring little change to the natural vegetation of this area. Rains that come from January to March simply allow the cover to become a little thicker and the grasses to lose some of their burnt appearance (Ogilvie, 1922:117).

On the eastern slopes of the Andes, meadows give way to dense, low forest, "Ceja de la Montaña," at elevations between approximately 9800 and 11,400 feet. Dense "eyebrow" forest covers most of the steep ridges and valleys, and taller "montaña" forest grows on the lower slopes and flat valley bottoms. "Eyebrow" and "montaña" gradually merge at approximately 3900 feet elevation (Ogilvie, 1922:119). Tree lines and vegetational types vary with topography and latitude. Arid regions occur in some of the eastern valleys due to the effects of rain shadows. The most extensive of these occurs along the Alto Río Marañón.

The hot, humid forest of the low country east and northeast of the Andes spreads eastward across the foothills into the true Amazonian lowland. This forest is characterized by tall trees with buttressed trunks, a dense, high canopy, and sparse undergrowth (Ogilvie, 1922:121).

ZOOGEOGRAPHIC COMMENTS

Few, if any, Peruvian localities have been collected adequately, and the relatively small number of bats available from Perú and critical adjacent areas does not warrant more than a preliminary zoogeographic discussion. The Amazonas region has attracted greatest attention, because of its faunal diversity, whereas the higher elevations of the Andes and the west coast have been largely neglected.

The physiographic and altitudinal distribution of Peruvian bats (based only on current records) is summarized in Tables 1 and 2. Further collecting undoubtedly will reveal wider distributions for some species presently known only from one or a few localities. The geographic distribution of bats in Perú is restricted primarily by a combination of extreme habitat differences and by the height and width of the Andean Cordillera. Distributional records indicate that 83 species are restricted to areas east of the Andes; 19 species occur on both sides. Three species and three subspecies (*Lonchophylla hesperia, Tomopeas ravus, Promops davisoni, Myotis nigricans nicholsoni, Molossus molossus daulensis, Eumops auripendulus auripendulus*) are restricted to west of the Andes.

It seems possible to divide Peruvian bats into three general categories: (1) those limited primarily to rainforest; (2) those restricted primarily to areas lacking rainforest (arid desert to savannah and dry forest); (3) widespread species not restricted to the two categories first listed. In the following discussion, bats are referred to as "rainforest," "non-rainforest," and "widespread" species, respectively.

TABLE 1. Approximate physiographic and altitudinal distribution of the 101 species of Peruvian bats known from east of the Andes based on locality records. Numbers in parentheses are number of species.

Taxa	Amazon plains and foothills to 3000 ft	3000 to 6500 ft	Broken mountain slopes, 3000 to above 10,000 ft: 6500 to 10,000 ft	above 10,000 ft
Emballonuridae	(1)			
	(8)			
Noctilionidae	(2)			
Phyllostomatidae				
Chilonycterinae	(2)			
Phyllostomatinae	(15)			
Glossophaginae		(2)		
		(1)		
	(8)			
		(1)		
Carolliinae		(1)		
	(3)			
		(1)		
Sturnirinae		(2)		
	(4)			
Stenoderminae		(1)		
		(2)		
	(13)		(1)	
		(1)		
Desmodontidae			(1)	
		(1)		
	(1)			
Furipteridae	(1)			
		(1)		
Thyropteridae	(2)			
Vespertilionidae			(3)	
		(2)		
		(1)		
	(5)			
			(1)	
Molossidae		(1)		
		(3)		
	(8)			
		(1)		

Of the 23 species recorded from west of the Andean Cordillera, present distributional knowledge indicates that 13 (including three, *Glossophaga soricina, Myotis nigricans,* and *Molossus molossus,* which have distinctive subspecies east and west of the Andes that are adapted to rainforest and non-rainforest environments, respectively) are widespread, six fall in the second category above, and four are rainforest species (see Table 3). The four mentioned last all are frugivorous and are known in western Perú only from the forested northwestern tip, whereas the insect-, nectar-, and blood-feeders are much more widely distributed. The 13 widespread species are insectivorous (10), nectivorous (2), or sanguivorous (1). The latter, the vampire

bat *(Desmodus rotundus)*, is probably the most diverse, ecologically, of all Peruvian bats. In the arid west, where it can subsist on the blood of sea birds, it often occupies areas that are completely devoid of either fresh water or vegetation. Among the six non-rainforest species, four are insectivorous, and two are nectivorous.

In winter, there is sufficient moisture along the coastal hills or "lomas" to support a large variety of flowering plants (Ogilvie, 1922:111). This provides the possibility of dispersal of nectar- and insect-eating bats between river valley oases. When the dew fails at the end of winter, the hills dry up and the plants wither or die within a short time, leaving only the river valleys habitable for most animal life. Even in these valleys there are no dependable sources of food for bats that are unable to subsist on nectar, insects, or blood.

Of the six non-rainforest species that occur in the Pacific arid regions of Perú and Ecuador, three *(Platalina genovensium, Amorphochilus schnablii,* and *Eptesicus innoxious)* are found east as well as west of the Andean Cordillera. East of the Cordillera these bats (except for *E. innoxius,* recorded only from Argentina in the east) are restricted to valleys, such as the Marañón, where rain shadows impose xeric conditions. The apparent absence of *Lonchophylla hesperia, Tomopeas ravus, Myotis nigricans nicholsoni,* and *Molossus molossus daulensis* east of the Andes may be actual or simply an artifact of inadequate collecting.

The trans-Andean distribution of at least 50 percent of the non-rainforest bat fauna of Perú, as well as the distribution of rainforest and widespread species, clearly implies the presence of a trans-Andean dispersal route in northern Perú. Furthermore, the amount of divergence found in related populations east and west of the Andes suggests varying degrees of isolation, due to a filtering effect.

After noting the distributional evidence for trans-Andean dispersal, I found that there were two trans-Andean passes of approximately 7000 to 8000 feet elevation near the Ecuadorian border of Perú and learned that these passes are thought to have been of major importance in determining the present distribution of both birds (Chapman, 1926; Haffer, 1967*a,b,c*) and reptiles (Schmidt and Walker, 1943).

One pass is located between the headwaters of the Río Piura and Río Huancabamba. A bat crossing this pass would have to travel six miles at elevations between 5000 and 6500 feet and about four miles at approximately 7000 feet. The other is located between the headwaters of the Río Chotano and Río Chancay; a bat crossing it would have to traverse 30 miles of elevatons between 5000 and 6500 feet and three miles between approximately 6500 and 8000 feet. Low, xeric forest occurs in both passes and along the adjoining river valleys (Tosi, 1960).

TABLE 2. Approximate physiographic and altitudinal distribution of Peruvian bats in high Andes (2 species) and west of Andes (21 species) based on locality records.

Taxa	Altiplano	Puna	NW forest	Arid regions, sea level to above 10,000 ft: Oases in coastal desert	3000 to 10,000 ft	above 10,000 ft
Emballonuridae		—(1)[1]—				
Phyllosomatidae						
Glossophaginae				———(1)———		
				—(3)—		
Stenoderminae			—(4)—			
Desmodontidae			————(1)————			
Furipteridae				—(1)—		
Vespertilionidae	—(1)[2]—			————(2)————		
				—(1)—		
				———(2)———		
Molossidae				—(6)—		

[1] *Centronycteris maximiliani* was reported from the high plains of Perú; no specific locality was given, and this record is in doubt.

[2] *Histiotus macrotus* has been reported from the low west coast as well as from near Lake Titicaca.

Either of these passes could be crossed easily in a single night, and several species of bats are probably at least seasonal residents in these passes. Of the 19 species known to occur both east and west of the Andes, eight already have been recorded from elevations of at least 6000 feet or higher, and there is little reason to doubt that others might move through the passes also. Bats such as *Anoura geoffroyi, Desmodus rotundus, Myotis chiloensis,* and *Lasiurus borealis* probably could disperse through the northern passes without hinderance and may be able to cross in other areas as far south as the Departamento de Cajamarca. South of there, the Andes increase greatly in both width and height and cannot be crossed at elevations below about 15,000 feet.

Uplift of the Andes severed the once continuous area of humid tropics in South America, leaving it in two disconnected areas. The pass in northern Perú formed by the headwaters of the Río Piura and the Río Huancabamba is the lowest pass between Amazonian and Pacific drainage in the entire Andean system from southern Chile to eastern Colombia, and, according to Chapman (1926:34, 44, 129-130), there probably is no interchange of tropical or subtropical life, direct or indirect, between the two divisions except for movement through the two northern Peruvian passes (mentioned above) and that at Andalucia in eastern Colombia. It is conceivable that such a high-elevation species as *Anoura geoffroyi* could occasionally cross the Andes through higher passes between northern Perú and eastern Colombia, but,

TABLE 3. Ecologic affinities of bats known from west of the Andean Cordillera in Peru.

Rainforest	Non-rainforest	Widespread
Uroderma bilobatum	*Lonchophylla hesperia*	*Glossophaga soricina*
Vampyrops vittatus	*Platalina genovensium*	*Anoura geoffroyi*
Vampyrops helleri	*Amorphochilus schnablii*	*Desmodus rotundus*
Artibeus jamaicensis	*Eptesicus innoxius*	*Myotis chiloensis*
	Tomopeas ravus	*Myotis nigricans*
	Promops davisoni	*Histiotus macrotis*
		Lasiurus borealis
		Tadarida brasiliensis
		Tadarida similis
		Mormopterus kalinowskii
		Molossus molossus
		Eumops auripendulus?
		Eumops perotis

for the most part, there appears to be no evidence that would argue against Chapman's conclusions.

The Peruvian and Colombian passes act as filters between the two divisions of tropical South America. Passes in both countries are associated with arid or semiarid regions, which greatly restrict the movement of rainforest-adapted animals. This habitat restriction, combined with the varied elevational tolerance of different species, doubtless has played an important role in determining bat distribution. In northern Perú, most species of bats never cross the Andes, whereas some, such as *Glossophaga soricina* and *Molossus molossus,* have crossed and formed trans-Andean subspecies, and others, already mentioned, may live in the passes or may even migrate seasonally through them.

Recent trans-Andean dispersal is particularly well illustrated by the ranges of *Platalina genovensium, Glossophaga soricina valens, Uroderma bilobatum thomasi* (see Davis, 1968), and *Amorphochilus schnablii.*

Pleistocene environmental fluctuations apparently greatly modified and possibly even reversed the influence of filtration. According to Haffer (1967*a*), repeated expansion and contraction of rainforest and non-rainforest vegetation have corresponded with alternating wet glacials and dry interglacials, respectively, during the Pleistocene, and alternating wet and dry periods have continued throughout post-Pleistocene times. After an extensive study of bird zoogeography and speciation in Colombia, Haffer (1968) concluded that "many if not most Colombian bird species inhabiting the uplands and lowlands today were differentiated during the Pleistocene rather than in Tertiary time." He suggested that isolation and subsequent differentiation of many bird populations was probably caused by the changing distribution of rainforest and non-rainforest vegetation. This interpretation is supported by the observations of Chapman (1926:62, 117) in Ecuador.

He found strikingly different avian faunas, with widely separated geographic origins, occurring side by side in rainforest and non-rainforest regions, and argued strongly against fortuitous dispersal. The meager information available suggests that the distribution and speciation of bats may be the result of events similar to those suggested for birds by Chapman (1926) and Haffer (1967*a,b,c,* 1968).

Along with the importance of rainforest and non-rainforest expansions and contractions during the Pleistocene, the overall cooling effects of glacial cycles must be considered. Though actual glaciation seldom extended below an elevation of approximately 12,000 feet in the Andes, lowered periglacial temperature may have had the effect of producing environments as low as 7000 feet that would occur today only at approximately 9000 feet in elevation. Such changes, correlated with rainforest and non-rainforest alternation, could exert a profound effect on trans-Andean bat movements. During an interglacial period a lowland non-rainforest species could extend its range through a pass and a subsequent glacial period could effect the complete isolation of segments east and west of the Cordillera. At the same time, it is conceivable that a species primarily associated with rainforest could have crossed from east to west at the beginning of an interglacial when the mean temperature might have risen more rapidly than the forest vegetation contracted. These rainforest-associated species would become isolated later during the interglacial, when the passes once more became dry and arid. Some species, which are able to occupy elevations of 9000 feet or higher and which are not restricted severely by rainforest or non-rainforest environments, may have been relatively unaffected by Pleistocene climatic changes. Bats such as *Anoura geoffroyi* and *Desmodus rotundus,* for example, which are known to occur at elevations of at least 9000 and 11,000 feet, respectively, and which are not noticeably restricted by "rainforest" or "non-rainforest" environments, occur commonly on both sides of the Andes without forming trans-Andean races. On the other hand, *Glossophaga soricina,* which has not been collected above 6000 feet, did form trans-Andean races. *G. s. valens,* which is arid-adapted, apparently differentiated in the west and subsequently reinvaded the east, where it is restricted to the arid environment of the Marañón Valley.

Knowledge of the 23 species of bats recorded from western Perú is extremely limited. Nevertheless, a discussion of the possible origin of this fauna is presented with the intent of stimulating further study of the significant problems involved. For purposes of discussion, the Pacific coast fauna can be divided into three general groups: (1) pre-Andean residents, (2) trans-Andean emigrants, and (3) coastal Ecuadorian emigrants.

Chapman (1926:45, 73), in his study of the arid-adapted bird fauna of Pacific Ecuador and Perú, found evidence that some formerly continuous

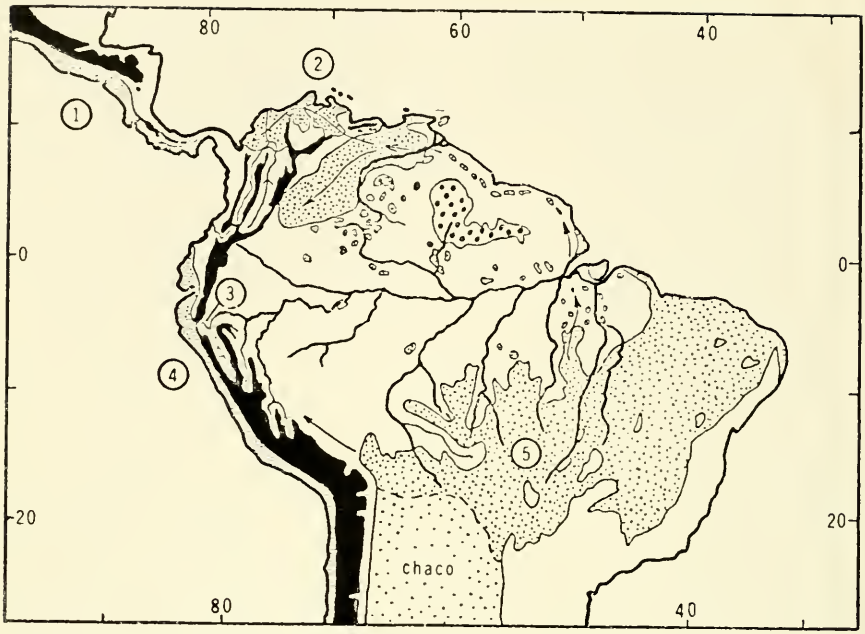

FIG. 2. Present distribution of non-forest vegetation in tropical South and Central America (modified after Haffer, 1967). Elevations higher than 1000 meters are in black. Open stipple represents the following: cerrado, campos and caatinga south of the Amazon River; chaparral and savannas of northern South and Central America with galley forests or small patches of deciduous woods, or both; semidesert and desert along the Pacific coast of South America. The savannas of the Guiana table mountains and of part of the surrounding lowlands are heavily stippled. White areas are forest. Arrows indicate advancing non-forest faunas during dry climatic periods of the Pleistocene and post-Pleistocene.

1, Central American non-forest region; 2, Colombian-Venezuelan non-forest region; 3, location of the arid Marañón Valley and north Peruvian passes; 4, arid Pacific coastal region; 5, Brazilian non-forest region. The campos just north of the lower Amazon river are more extensive than indicated on the map.

populations had been broken by the elevation of the Andes. He concluded that the most distinctive forms were pre-Andean, and "hence that prior to the elevation of the Andes this region was, in part at least, arid or semi-arid." Schmidt and Walker (1943), however, in a study of the reptiles of coastal Perú, concluded that despite a large number of endemics, the arid coast seemed clearly to be a relatively recent desert, in which there had not been time for the evolution of specifically "xerocole" types. Information presented by Ogilvie (1922:109) seems to corroborate Schmidt's interpretation.

Platalina genovensium, Amorphochilus schnablii, and *Tomopeas ravus* seem likely to have occupied an arid or semiarid coastal region for a considerable period of time. Chapman's (1926:51) work seems to indicate that most post-Andean evolution of birds in western Ecuador has not yet

reached the generic level. In contrast, *Tomopeas ravus,* which is arid-adapted and represents a distinctive subfamily, indicates a relatively long period of divergence. *T. ravus* may be at least distantly related to *Rhogeesa tumida* (Miller, 1900*b*), which inhabits both rainforest and non-rainforest environments of northern South America. The nearest living relatives of *Platalina genovensium* and *Amorphochilus schnablii* are *Lonchophylla mordax* (Thomas, 1928*a*) and *Furipterus horrens,* respectively. Both *L. mordax* and *F. horrens* are widely distributed from Panamá south through Brazil, and both have been reported from the Peruvian Amazonas. Neither, however, has been reported from western Ecuador. This distribution may have resulted from east-west splitting of continuous ancestral populations during uplift, or from early trans-Andean emigration. Both *P. genovensium* and *A. schnablii* have subsequently crossed the Andes from west to east to invade at least the arid Marañón Valley. Such west coast divergence and subsequent trans-Andean dispersal into the Marañón Valley also has been observed in a number of birds (Chapman, 1926:73).

Present knowledge of ecological and elevational requirements of Peruvian bats, combined with a consideration of Pleistocene environments, indicates that the trans-Andean passes of northern Perú may have played an important role in speciation. Haffer (1967*a,c*) made an extensive study of the probable routes of dispersal and divergence of non-rainforest birds and concluded that a number of species moved northward from southern Brazil, Bolivia, and Argentina. This northward dispersal apparently followed two main routes, both of which were at least partially dependent on interglacial expansion of non-rainforest environments. One route followed the east coast of Brazil, the Guianas, and Venezuela into northern Colombia. The other, of much greater importance to the Peruvian fauna, followed the eastern border of the Andes to the Marañón Valley, whence it crossed via the passes in northern Perú to the Pacific coast of Perú and Ecuador (see Fig. 2). According to Haffer (1967*c*), both routes have enhanced the fauna of Colombia north of the Andes.

The western route, which follows the eastern slopes of the Andes to northern Perú, owes its existence to a combination of large, arid, inter-Andean valleys and the probable expansion of non-rainforest environments during interglacials. Haffer (1967*a*) suggested that dry pockets along the eastern side of the Andes established a "discontinuous connection of the non-[rain]forest restricted Brazilian fauna with the Marañón and the arid Pacific." Several species of bats appear to corroborate such a hypothesis.

Although I have been unable to locate ecological data, perusal of distributional records seems to indicate that both *Promops nasutus* and *Promops occultus* inhabit non-rainforest areas. *P. nasutus* is known from Brazil, Paraguay, and Argentina, and *P. occultus* is known only from Paraguay.

Promops davisoni from western Perú appears to be closely allied to, and somewhat intermediate between, *P. nasutus* and *P. occultus* (Thomas, 1921). The most likely hypothesis for explaining this distribution appears to be trans-Andean dispersal in northern Perú with subsequent isolation and divergence. A similar example is that of *Eptesicus dorinus* and *Eptesicus innoxius;* the former occurs in Argentina, eastern Brazil, Paraguay, and Uruguay, and the latter occurs in western Perú and Ecuador and possibly in Argentina (Villa-R. and Villa Cornejo, 1969). If, indeed, *E. innoxius* does occur in northern Argentina, such a distribution provides additional evidence of trans-Andean dispersal in northern Perú. It is possible that *E. innoxius* underwent isolation and divergence in western Perú and Ecuador and subsequently reinvaded the east. Further collecting in the Marañón and Urubamba valleys may provide valuable evidence concerning the zoogeographic history of this bat. Further evidence for trans-Andean dispersal of bats in northern Perú is provided by the geographic distributions of *Eumops auripendulus, Eumops perotis,* and possibly also *Vampyrops helleri.*

Unfortunately, little is known concerning the bat fauna of Ecuador. Some species not yet known to occur in that country probably will be found to have continuous distributions between Colombia and northwestern Perú. If true, however, this still would not rule out the possible importance of the northern Peruvian passes in providing avenues of dispersal across the Andes prior to northward movement (see distribution of *Crax rubra*—Haffer, 1967*c*).

Actually, the contrasting rainforest and non-rainforest environments of northern and southern Ecuador, respectively, probably prevent many species of bats from occupying both of those regions. Chapman (1926:46) found that 50 species of Colombian Pacific birds reach the limit of their distributions in northwestern Ecuador. Many birds of the Colombian Pacific fauna occur no farther south than the divide between the Esmeraldas and Guayaquil drainage systems, and several species are represented north and south of the divide by different races (Chapman, 1926:55). South of this point the avian fauna shows "some obvious relations to the Brazilian non-[rain]forest fauna" and "very restricted relations to the non-[rain]forest faunas of northern South and Central America (Haffer, 1967*a*)." Further study of the Pacific coast bat fauna likely will reveal a similar discontinuity. The evidence now available suggests that the arid-adapted bat fauna of the Pacific coastal region of Perú and Ecuador is considerably more closely allied faunally to Brazil than to Colombia. This does not exclude the possibility that some members of the Pacific fauna are of northern origin. Several authors currently are reviewing the genus *Artibeus,* and the zoogeographic affinities of *Artibeus fraterculus* and *A. jamaicensis* will be of considerable interest. Pacific populations of these bats may have been de-

rived from either Colombia or Brazil, and quite possibly from both places.

The validity of my hypotheses may be tested through faunal analysis (1) in western Ecuador (especially north and south of the Esmeraldas and Guayaquil drainage systems), (2) in, and on both sides of, the low passes in northern Perú and eastern Colombia, (3) in the arid valleys of the Río Marañón, Río Urubamba, Río La Paz, Río Grande, Río Pilcomayo, and other river systems, and (4) in the non-rainforest areas of Argentina, southern Brazil, Bolivia, and Paraguay. Additionally, studies of the distributional restrictions imposed by elevation and by rainforest as opposed to non-rainforest environments would prove significant.

To summarize, trans-Andean passes in northern Perú are the lowest and most easily accessible to be found in the entire Andean system between southern Chile and eastern Colombia. The pass between Río Piura and Río Huancabamba (7000 feet in elevation) in northern Perú forms a complete barrier to most lowland species of bats while acting as a filter zone for some species and allowing free passage to others. The selectivity of this route of dispersal likely has been considerably altered and possibly even reversed during consecutive wet glacial and dry interglacial periods of the Pleistocene. Such a dual action of elevation and climate provides a possible mechanism whereby isolation and divergence could have occurred.

Preliminary examination of distributional records of bats and comparison with those of better known avian faunas, seems to suggest the following: (1) some Pacific coast populations are of pre-Andean origin; (2) considerable divergence at the specific and subspecific levels has resulted from Pleistocene and post-Pleistocene trans-Andean dispersal and isolation; (3) the Pacific coastal fauna is more closely allied to Brazilian faunas than to those of Colombia and northern Ecuador.

Present knowledge concerning the ecology, distribution, and systematics of South American bats is far from complete. Hence, the zoogeographic conclusions presented herein are based upon limited knowledge and should be regarded only as tentative hypotheses that provide a basis for further investigation.

SPECIES ACCOUNTS

Family **EMBALLONURIDAE**

Rhynchonycteris naso (Wied-Neuwied)

Distribution. Occurs along rivers throughout Amazonas; recorded from Contamana and San Jeronimo, 500 feet, Río Ucayali, Departamento de Loreto (Thomas, 1928*b*), south to Alto Río Marañón (no exact locality, AMNH 169952-53), and Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Remarks. On the Río Azupizu these bats roosted in groups of 5-20 individuals on the shaded parts of trees or old logs that protruded over water.

Reproduction. 21-22 July: 2 pregnant females (c-r lengths 18, 23). 1 non-pregnant female, 2 males (testes 3.5 x 2, 5 x 3). 10 August: 1 non-pregnant female. 18 August: 1 male (testes 6 x 4).

Specimens collected (15). San Juan, 11 (7 USNM); San Pablo, 4.

Saccopteryx bilineata (Temminck)

Distribution. Occurs throughout Amazonas; recorded from Contamana, 500 feet, Río Ucayali, Departamento de Loreto (Thomas, 1928*b*), south to Huajyumbe, near Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Remarks. Colonies of 5-30 individuals of this species were found in hollows formed by large vines growing against tree trunks, and in hollow logs. A hollow log in which nine individuals were captured had an inside diameter of 4½ feet, a length of 25 feet, and was open at only one end. It was lying on the ground, but the opening in the butt of the log was 6 feet above the ground. The foliage above was relatively thin, allowing light to enter. Vegetation in the surrounding area was second growth jungle; other roosts were found, however, in dense, heavily shaded areas in mature forest. In hollow trees these bats roosted within a few feet of *Carollia perspicillata, Micronycteris megalotis,* and *Micronycteris hirsuta.* The greater white-lined bat was one of the commonest bats at San Pablo and San Juan where it was usually among the earliest flyers after sundown and also was shot while feeding only a few minutes before sunrise.

Reproduction. 27 June: 1 pregnant female (c-r length 6.5). 21 July: 1 pregnant female (c-r length 16), 1 non-pregnant female. 26 July: 1 pregnant female (c-r length 9), 1 non-pregnant female. 5 August: 1 pregnant female (c-r length 20). 10 August: 12 pregnant females (c-r lengths 12-20, av. 15.7), 7 non-pregnant females, 7 males (testes 2 x 1 to 5 x 4, av. 3 x 1.9). 14-16 August: 3 non-pregnant females, 1 male (testes 3 x 2). 18-19 August: 12 pregnant females (c-r lengths 14-22, av. 19.1), 5 males (testes 3 x 2 to 4 x 2, av. 3.2 x 2). 25 August: 5 pregnant females (c-r lengths 14-20, av. 17.8), 4 non-pregnant females.

Specimens collected (100). San Juan, 73 (71 USNM and many others discarded); San Pablo, 26; San Ramón, 1.

Saccopteryx canescens Thomas

This bat is known in Perú from a single specimen taken at Puerto Victoria, Río Pachitea, Departamento de Huánuco (Sanborn, 1937).

Saccopteryx leptura (Schreber)

Distribution. Occurs throughout Amazonas and to elevations of at least 3000 feet in Andes (Thomas, 1893); recorded from Pebas, Río Amazonas, Departamento de Loreto (Thomas, 1928*c*), south to Bellavista [Bella Vista], Río Apurimac, Departamento de Cuzco (Sanborn, 1937). According to Sanborn's distribution map, Bellavista should be approximately on the border between the departments of Cuzco and Madre de Dios in southern Perú. There are two towns named Bella Vista near the site indicated; the most distant is about 108 kilometers east of the Peruvian border on the Río Tahuamanu, Brazil; the nearest is about 400 kilometers SSW Machu Picchu, Río Apurimac, Departamento de Cuzco, and is apparently the locality to which Sanborn referred.

Remarks. Five individuals were found near San Juan roosting together 25 feet up on the side of a tree in mature evergreen forest; the tree was 2½ feet in diameter.

Reproduction. 10-11 August: 1 non-pregnant female, 3 males (testes 4 x 3, 4 x 2, 3 x 2). 25 August: 1 male (testes 3 x 2).

Specimens collected (5). San Juan, 5.

Cormura brevirostris (Wagner)

Distribution. Known from *Puerto Indiana, near Pebas, Río Amazonas, Departamento de Loreto (Sanborn, 1937); Tingo Maria, Río Huallaga, Departamento de Huánuco (Sanborn, 1936); south to Río Inambari in southern Perú (no exact locality, departamento not specified—Thomas, 1913*a*).

Remarks. Two individuals from San Juan were collected by Campa Indians from a hollow tree in which a small colony of *Saccopteryx bilineata* also roosted.

Reproduction. 20 August: 2 males (testes 4 x 3, 3 x 2).

Specimens collected (2). San Juan, 2.

Peropteryx kappleri Peters

Distribution. Known from Marcapata, Departamento de Cuzco (Sanborn, 1951*b*), and from San Juan.

Remarks. Specimens taken at Marcapata were described as *Peropteryx kappleri intermedius* by Sanborn because they were intermediate in size between *P. k. kappleri* Peters and *P. macrotis*

(Wagner). Forearm lengths of Sanborn's four specimens were 45.4-49.5. The specimen here reported from San Juan (forearm 48.2), where *P. macrotis* also occurs, extends the known Peruvian range of this bat approximately 525 kilometers to the northwest.

My one specimen was shot from among many other similar bats that were in flight after being disturbed in a large but shallow cave in mature evergreen forest. The cave opened beneath large boulders in which many cracks and crevices were found; a stream flowed from the opening. *Phyllostomus hastatus* and *Vampyrops vittatus* were collected in the same cave.

Reproduction. 16 August: 1 non-pregnant female.

Specimen collected (1). San Juan, 1.

Peropteryx macrotis (Wagner)

Distribution. Known from *Puerto Indiana, near Pebas, Río Amazonas (Sanborn, 1937), and from Lagarto, Río Ucayali (Thomas, 1920*b*), both in Departamento de Loreto, south to Machu Picchu, Departamento de Cuzco (Thomas, *loc. cit.;* Sanborn, *loc. cit.*), and La Pamapa, Departamento de Puno (Sanborn, 1951*b*).

Remarks. Ten specimens were shot from a cluster of about 25 found roosting under a root ledge over a small stream in mature forest. Two were netted, and another was shot as it fed over a small garden at dusk. The subspecies reported from Perú is *P. m. macrotis* (Wagner).

Reproduction. 21 July: 1 male (testes 3 x 1). 11 August: 3 pregnant females (c-r lengths 6, 11, 13), 2 males (testes 2 x 1, 2 x 1).

Specimens collected (13). San Juan, 12; San Pablo, 1.

Peronymus leucopterus (Peters)

This bat is recorded from Perú only from Tushemo [Tushma], near Masisea, Río Ucayali, Departamento de Loreto (Thomas, 1924). The single specimen was described by Thomas as *P. cyclops,* which equals *P. leucopterus cyclops* (Sanborn, 1937). Cabrera (1958:52) placed *Peronymus* as a subgenus of *Peropteryx.*

Centronycteris maximiliani (Fischer)

This species was reported from the high plains of Perú by Taczanowski (Peters, 1872), but no specific locality was given.

Diclidurus albus Wied-Neuwied

A single specimen was examined from Parimari [Parinari], Río Amazonas, Departamento de Loreto (AMNH 99310).

Diclidurus scutatus Peters

A specimen in the American Museum of Natural History (AMNH 99309) is labeled as from Perú but lacks additional locality data.

Family **NOCTILIONIDAE**

Noctilio labialis (Kerr)

Distribution. Occurs along rivers throughout Amazonas; known from Yurimaguas, 600 feet, Río Huallaga (Osgood, 1914) and from Pucallpa, Río Ucayali (Sanborn, 1949*b*), both in Departamento de Loreto, south to *Luisiana, Río Apurimac, Departamento de Cuzco (AMNH 208055-208057).

Remarks. These bats were observed and captured especially at dusk, when groups of 8-15 individuals would fly up the Río Azupizu 2-7 feet above the water and about 25 feet from shore. The subspecies reported from Perú is *N. l. zaparo* Cabrera.

Reproduction. 21 July: 2 pregnant females (c-r lengths 14, 16), 1 non-pregnant female, 1 male (testes 7 x 4). 26 July: 1 male (testes 5 x 8).

Specimens collected (7). San Juan, 2 (AMNH); San Pablo, 5.

Noctilio leporinus (Linnaeus)

Distribution. Probably occurs along large rivers throughout Amazonas; recorded from Pebas, Río Amazonas (Thomas, 1928*c*), south to Cumeria [Cumaria] (Thomas, 1928*b*), Yarinacocha, and Pucallpa (Sanborn, 1949*b*), Río Ucayali, Departamento de Loreto.

Remarks. Some of these fish-eating bats were lured into mist nets by treating the water along the edge of the Río Azupizu with barbasco (a native fish poison). The barbasco killed many small minnows, which floated to the surface and attracted the bats. Campa Indians report that large numbers of these bats often congregate at places where fish are being poisoned at night. *N. l. leporinus* (Linnaeus) is the subspecies reported from Perú.

Reproduction. 7 July: 1 pregnant female (c-r length 38). 19 July: 1 pregnant female (young born in captivity). 21 July: 1 male (testes 8 x 5). 26 July: 1 non-pregnant female.

Specimens collected (10). San Juan, 7 (1 USNM); San Pablo, 3.

Family **PHYLLOSTOMATIDAE**

Pteronotus parnellii (Wagner)

Two specimens of *P. p. rubiginosus* (Wagner) collected at Tingo Maria, 2000 feet, Río Huallaga, Departamento de Huánuco (Thomas, 1927*b*), are the only Peruvian records known to me. Jones (1966) and several others before him gave reasons for use of the specific name *parnellii* rather than *rubiginosus*.

Pteronotus suapurensis (J. A. Allen)

This naked-backed bat has been reported from Yarinacocha, Río Ucayali, Departamento de Loreto by Sanborn (1949*b*). The subspecific status of this species in Perú is not clear.

Micronycteris behni (Peters)

This bat has been recorded from Perú only from the Río Cosnipata, Distrito and Departamento de Puno (Andersen, 1906).

Micronycteris hirsuta (Peters)

Distribution. Known only from San Juan.

Remarks. Specimens collected near San Juan are the first records of this bat from Perú. The nearest previous localities of record are Magdalena, Colombia (Hershkovitz, 1949), and British Guiana [Guayana] (Hill, 1964).

Three big-eared bats were shot from a group of six that were roosting singly about 15 feet up inside a hollow tree. The bats may have been in a cluster before they were disturbed. There was an opening on the tree, near the ground, that was 2 feet high and 1 foot wide, and another opening about 1 foot in diameter some 25 feet up, where the hollow ended. The cavity in which the bats were shot was 3 feet in diameter at the base and narrowed to about 2 feet in diameter near the top. *Carollia perspicillata* and *Saccopteryx bilineata* were also collected in this roost.

Reproduction. 26 July: 1 pregnant female (c-r length 19), 1 non-pregnant female, 1 male (testes 4 x 2).

Specimens collected (3). San Juan, 3.

Micronycteris megalotis (Gray)

Distribution. Occurs throughout Amazonas; recorded from Yarinacocha, Río Ucayali, Departamento de Loreto (Sanborn, 1949*b*), south to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*), and to an elevation of at least 3000 feet in Andes at Chinchavita, Departamento de Huánuco (Thomas, 1927*b*).

Remarks. I found bats of this species roosting under a root ledge above a stream, in fallen logs, and in hollow trees, where they formed clusters of 5-25 individuals. One roost was inside a hollow tree 4 feet in diameter and more than 100 feet tall. Bats appeared to enter through a hole (2 feet high and 6 inches wide) in the base. The tree was in a relatively open area and was surrounded by dense vines. The Peruvian subspecies is *M. m. megalotis* (Gray).

Reproduction. 28 June: 1 male (testes 2 x 1.5). 13 July: 1 male (testes 1 x 1). 10-11 August: 1 pregnant female (c-r length 25), 2 non-pregnant females, 1 male (testes 2 x 1). 12-13 August: 1 pregnant female (c-r length 20), 12 non-pregnant females, 4 males (testes 3 x 2, 2 x 1, 1.5 x 1, 1 x 0.5). 14 August: 1 male (testes 1.5 x 1). 19-21 August: 2 males (testes 2 x 1, 2 x 1). 23 August: 5 non-pregnant females, 1 male (testes 2 x 1).

Specimens collected (61). San Juan, 58 (USNM); San Pablo, 2; San Ramón, 1.

Micronycteris minuta (Gervais)

Distribution. Known only from San Pablo.

Remarks. Two *M. minuta* collected near San Pablo are the first Peruvian records. Cucuta, Colombia (Sanborn, 1949*a*), and Pará and Santa Catherina, Brazil (Andersen, 1906), represent the localities nearest Perú whence specimens have been reported previously. Both Peruvian specimens were netted in mature evergreen forest where Campa Indians had cleared most of the low vegetation to facilitate gathering of rubber from the larger trees.

Reproduction. 9 July: 1 non-pregnant female. 16 July: 1 non-pregnant female.

Specimens collected (2). San Pablo, 2.

Micronycteris nicefori Sanborn

Four specimens reported from *[Puerto] Indiana, Río Amazonas, Departamento de Loreto (Pirlot, 1968) provide the only record of the white-lined forest bat from Perú.

Barticonycteris daviesi Hill

Distribution. Known only from San Juan.

Remarks. Until three specimens were collected near San Juan, *B. daviesi* was known only by the holotype, captured on 3 December 1963, at a place 24 miles from Bartica, British Guiana [Guayana] (Hill, 1964). Peruvian specimens (USNM 364256-364257) extend the known range of this bat approximately 2650 kilometers to the southwest.

Specimens from Perú correspond closely with Hill's description of the holotype from Guayana. Two of the *B. daviesi* had entirely pigmented wings, but one male had an unpigmented stripe about half an inch wide on each wing along the body. The same individual also had unpigmented wing tips. External measurements of a female and two males are, respectively: total length, 90, 82, 91; length of tail, 7, 5, 7; length of hind foot, 20, 19, 19; length of ear, 31, 28, 29; length of forearm (dry), 53.8, 58.1, about 58 (wings spread); weight, 34 (pregnant), 24, 27. Unfortunately, all three skulls were damaged by shotgun pellets.

According to our reliable Campa Indian collector, Carlos Perez, the three *B. daviesi* were shot while roosting together in a hollow tree in mature forest.

Reproduction. 14 August: 1 pregnant female (c-r length 33), 2 males (testes 5 x 4, 4 x 3).

Specimens collected (3). San Juan, 3 (USNM).

Lonchorhina aurita Tomes

Distribution. This species has been taken only at San Juan.

Remarks. Five specimens from San Juan are the first to be recorded from Perú. The nearest localities of record previously reported were the Canal Zone, Panamá (Handley, 1966*b*), San Estaban, Venezuela (Anthony, 1923), Pará, Brazil (Vieira, 1942:305-306), and San Matais, Bolivia (Sanborn, 1932*a*).

All specimens were netted over trails in mature evergreen forest near the Río Azupizu. They differ from *L. occidentalis* (Anthony, 1923), described from Guayas, Ecuador, in having longer ears and forearms and in lacking blotches of ivory-yellow on the posterior margins of the wings. The following measurements were recorded from three Peruvian specimens (a male and two females, respectively); forearm 53.4, 53.7, 56.0; ear from notch 31, 32, 32. Measurements of the holotype of *L. occidentalis* (as given by Anthony) are, respectively, 48.7 and 25.5.

Unfortunately, *L. occidentalis* (Anthony) was omitted by Cabrera (1958) from his check list; however, recent authors (Goodwin and Greenhall, 1961:233; Hall and Kelson, 1959:104; Handley, 1966*b*; Jones, 1966) have followed Sanborn (1932*a*) in referring to *L. occidentalis* as a subspecies of *L. aurita*. Lacking adequate comparative material, specimens from Perú are tentatively classified as *L. a. aurita,* despite the fact that the forearms are longer than the longest thus far recorded for the species from other parts of its range.

Reproduction. 23 July: 1 lactating female. 25 July: 1 male (testes 4 x 2). 11 August: 1 non-pregnant female.

Specimens collected (5). San Juan, 5 (2 USNM).

Macrophyllum macrophyllum (Schinz)

Distribution. Recorded from mouth of Río Cenipa, Departamento de Amazonas (AMNH 98761), from San Jeronimo (Thomas, 1928*b*) and Yarinacocha (Sanborn, 1949*b*), Río Ucayali, Departamento de Loreto, and herein from San Juan.

Remarks. One long-legged bat was netted over a small stream in mature forest.

Specimen collected (1). San Juan, 1 (USNM).

Tonatia bidens (Spix)

The only specimen thus far recorded from Perú was obtained at Lagarto, Alto Ucayali, Departamento de Loreto (Goodwin, 1942).

Tonatia silvicola (D'Orbigny)

Distribution. Known throughout Amazonas; recorded from Pebas, Río Amazonas, Departamento de Loreto (Thomas, 1928*c*), south to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*), and to an elevation of 3000 feet in Andes at Chinchavita, Departamento de Huánuco (Thomas, 1927*b*).

Remarks. Four colonies of this species, consisting of 6-10 individuals each, were found roosting in hollow termite nests in mature evergreen forest. A Campa Indian collected 18, which he said came from a hollow tree. For further information see remarks in account of *Phyllostomus hastatus*. The subspecies reported from Perú is *T. s. silvicola* (D'Orbigny).

Reproduction. 8 July: 1 pregnant female (c-r length 21), 1 male (testes 5 x 3). 12 July: 1 pregnant female (c-r length 16), 1 male (testes 7 x 4). 23 August: 2 pregnant females (c-r length both 30), 21 males (testes 10 x 7 to 6 x 4, av. 8 x 5.9).

Specimens collected (34). Nevati, 2; San Juan, 28 (USNM); San Pablo, 4.

Mimon crenulatum (É. Geoffroy St.-Hilaire)

Distribution. Known from Pebas, Río Amazonas (Thomas, 1928*c*) to Yarinacocha, Río Ucayali (FMNH 62119-62120), both in Departamento de Loreto, and from San Juan.

Remarks. All but one of our specimens were netted in mature evergreen forest where Campa Indians had cleared away most of the low vegetation to facilitate the gathering of rubber from the larger trees. Four of the six specimens collected among the rubber trees were attracted when the first individual captured was induced to squeal. This method of attracting bats to the nets was successful for other species as well. The Peruvian subspecies is *M. c. longifolium* Wagner, of which *M. peruanum* Thomas is a synonym (see Handley, 1960).

Reproduction. 15-16 July: 1 pregnant female (c-r length 17), 3 males (testes 5 x 4, 5 x 3, 4 x 2). 25 July: 1 pregnant female (c-r length 13). 25 August: 1 male (testes 6 x 5).

Specimens collected (9). San Juan, 2 (1 USNM); San Pablo, 7.

Phyllostomus elongatus É. Geoffroy St.-Hilaire

Distribution. Occurs throughout Amazonas; first vaguely reported as occurring north of 10° latitude (Tschudi, 1844:68) and later recorded from Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Remarks. Colonies of from 7-15 individuals were encountered in large hollow trees in dense mature forest. One roost was found in a hollow tree with a base diameter of about 20 feet and a height of more than 100 feet. The tree was on the top of a hill in mature evergreen forest. Its base had two openings both about 2 feet wide and 4 feet high leading into a cavity; the inside diameter was 5 feet at the base but narrowed (60 feet up the tree) to about 3 feet. About 2 feet below the top of the main cavity there was another opening to the outside, allowing light to enter. Slightly above that opening was a hollow limb about 2 feet in diameter and 20 feet long with another opening at its far end. *P. elongatus* roosted at the top of the main cavity. More than 50 *Carollia perspicillata* roosted in cracks in the decaying sides from 5 feet above the ground level to within approximately 10 feet of the *P. elongatus,* and about 20 *Saccopteryx bilineata* were roosting in the hollow from just inside the lower entrances to about 30 feet high. Two shots fired up inside the hollow from my 12-gauge shotgun (dust shot), brought down seven *P. elongatus* along with *Carollia* and *Saccopteryx*. Additional *P. elongatus* were probably present, but some bats evidently escaped into the hollow limb. Two more shots brought down only *Carollia* and *Saccopteryx*.

P. elongatus were most often netted in or near garden plots where bananas were grown; the heads of netted individuals frequently were covered with yellow pollen. Captives, induced to squeal, quickly attracted additional individuals of both *P. elongatus* and *P. hastatus*.

Reproduction. 6-7 July: 1 pregnant female (c-r length 10), 2 non-pregnant females, 1 male (testes 6 x 3). 9 July: 1 male (testes 6 x 4). 11 July: 1 male (testes 4 x 5). 16 July (specimens from described roost): 2 pregnant females (c-r length 16 and 22), 2 non-pregnant females, 3 males (testes 6 x 3, 6 x 3, 4 x 3). 20 July: 2 males (testes 5 x 3, 3 x 2). 23 July: 1 pregnant female (c-r length 21), 1 male (testes 6 x 3). 25 July: 2 pregnant females (c-r length 20). 13 August: 1 male (testes 8 x 6). 27 August: 1 pregnant female (c-r length 33).

Specimens collected (31). San Juan, 15 (9 USNM); San Pablo, 16.

Phyllostomus hastatus (Pallas)

Distribution. Common throughout Amazonas; recorded from Shapaja, Juan Guerra, Tarapato, *Rumisapa and the Río Ponasa, all in the Departamento de San Martín (Jamet and Vasquez, 1957), south to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Remarks. These bats were found in colonies of 10 to 100 or more individuals, depending on the size of the roosting place. They were collected from hollow trees and termite nests, caves, and palm-thatched roofs. On the ceilings of caves this bat usually was found in clusters of 10-30 individuals. No roosts of *Tonatia sylvicola* were found that did not contain one or two *P. hastatus;* both sexes were encountered in *Tonatia* roosts. *P. hastatus* was most often netted around the edges of villages, especially near gardens where bananas were grown. Netted specimens were frequently at least partially covered with pollen. The subspecies reported from Perú is *P. h. curaca* Cabrera.

Reproduction. 15-17 June: 1 non-pregnant female, 7 males (testes 4 x 2 to 8 x 5, av. 6 x 4). 1-6 July: 19 males (testes 4 x 3 to 9 x 5, av. 6.5 x 4). 19 July: 1 male (testes 9 x 5). 16 August: 12 pregnant females (c-r length 22-30, av. 27.4), 8 non-pregnant females, 4 males (testes 8 x 5, 8 x 4, 7 x 5, 5 x 3).

Specimens collected (119). Nevati, 29; San Juan, 86 (82 USNM); San Pablo, 4.

Trachops cirrhosus (Spix)

Distribution. Known in Perú from Tushemo [Tushma], near Masisea, Río Ucayali, Departamento de Loreto (Thomas, 1928*b*), and from San Juan. There is also a specimen labeled "Rio Maranon, Pebas" (FMNH 29450). This individual probably was collected at Pebas, Río Amazonas, Departamento de Loreto.

Remarks. One of the two specimens collected was netted over a trail where many vines grew in mature forest by a stream. The other was netted at the edge of a large clearing, which had been virgin forest until the day before when it was cleared to lengthen an airstrip. The Peruvian subspecies is probably *T. c. cirrhosus* (Spix), which has been reported from northern Brazil, Colombia, the Guianas, Venezuela, and Panamá.

Reproduction. 25 July: 1 pregnant female (c-r length 17).

Specimens collected (2). San Juan, 2 (1 USNM).

Vampyrum spectrum (Linnaeus)

Linnaeus' false vampire bat is probably widely distributed in Amazonas and along the eastern slopes of the Andes, but it has been recorded from Perú only twice. The records are from Yarinacocha, Río Ucayali, Departamento de Loreto, and from Cosñipata, Paucartambo region, Departamento de Cuzco (Sanborn, 1949*b*). *V. s. spectrum* is the subspecies reported from Perú.

Glossophaga soricina (Pallas)

Distribution. Occurs throughout the lowlands of Perú on both sides of Andes; recorded east of Andes from Pebas, 330 feet, Departamento de Loreto (Thomas, 1928*c*), south to Idma, 6000 feet, Departamento de Cuzco (Thomas, 1920*b*), and west of Andes from Zorritos, Departamento de Tumbes (G. M. Allen, 1908), south to Valle del Tambo, Departamento de Arequipa (de la Puente, 1951:8-9).

Remarks. Near San Ramón these bats were found roosting in clusters of four to eight individuals in a cement drain beneath a sawmill. They roosted near similar clusters of *Carollia perspicillata. G. soricina* was taken at Nevati in nets set among blooming cashew trees. Two subspecies are recorded from Perú, *G. s. soricina* (Pallas) to the east of the Andes in Amazonas and *G. s. valens* (Miller) to the west of the Andes and also in the arid Marañón Valley.

Reproduction. 27 June: 2 non-pregnant females, 1 male (testes 5 x 3). 5-7 July: 1 non-pregnant female, 2 males (testes 7 x 5, 6 x 4). 16 July: 1 pregnant female (c-r length 10), 1 male (testes 6 x 5). 26 July: 1 male (testes 4 x 2.5). 10-19 August: 1 non-pregnant female, 5 males (testes 5 x 4, 5 x 4, 5 x 4, 4 x 3, 4 x 3).

Specimens collected (25). Nevati, 7; San Juan, 8 (7 USNM); San Pablo, 3; San Ramón, 7.

Lonchophylla hesperia G. M. Allen

The only Peruvian records are west of the Andes from Zorritos, Departamento de Tumbes (G. M. Allen, 1908), and from an unspecified locality in the Departamento de La Libertad (USNM 283177).

Lonchophylla mordax Thomas

An individual obtained at *[Puerto] Indiana, Río Amazonas, Departamento de Loreto (Pirlot, 1968), is the only record known from Perú. Pirlot used the specific name *concava* for this species, which is a synonym of *mordax* (see Handley, 1966*b*).

Lonchophylla robusta Miller

Distribution. Known only from San Juan and San Ramón.

Remarks. A specimen from San Ramón and another from San Juan are the first to be recorded south of San Gil and Sasaima, Colombia (Sanborn, 1941). The two Peruvian specimens differ from typical *robusta* in being larger, having a narrow interfemoral membrane, and possessing a short, sparse (but distinct) fringe of hairs along the posterior edge of the interfemoral membranes, and are only tentatively referred to that species. External measurements of a male and female are, respectively: total length, 80, 84; length of tail, 5, 6; length of hind foot, 14, 14; length of ear, 17, 17; length of forearm, 45.9, 45.4; weight, —, 16. Cranial measurements of the female are as follows: greatest length 27.0; depth of braincase 8.0; zygomatic breadth 11.3; breadth of braincase 10.4; interorbital breadth 5.3; length of maxillary toothrow 10.0; palatal breadth 6.6; palatal length 7.8.

A male was netted beneath a small clump of banana trees in an area of secondary growth near steeply rising hillsides and virgin evergreen forest. One female was taken at the edge of mature evergreen forest where many large trees had been cut the previous day to enlarge an airstrip.

Reproduction. 28 June: 1 male (testes 3 x 2). 5 August: 1 non-pregnant female.

Specimens collected (2). San Juan, 1 (USNM); San Ramón, 1.

Platalina genovensium Thomas

This rare bat has been recorded west of the Andes from Sullana, Departamento de Piura (Aellen, 1965), vicinity of Lima, Departamento de Lima (de la Puente, 1951:13), and Caravelli [Caraveli], Departamento de Arequipa (USNM 268765 and de la Puente, 1951:13), and east of the Andes from Huanaco [Huánuco], Departamento de Huánuco (Sanborn, 1936 and de la Puente, 1951:13-14).

Lionycteris spurrelli Thomas

Distribution. Known from Nevati, San Juan, and San Pablo. Additionally, a specimen in the American Museum of Natural History (AMNH 145504) is labeled *"Peru: Quincemil, 2000 ft."

Remarks. Specimens here reported are the first to be recorded from Perú. The nearest previous localities of record are Condota, Chocó, Colombia (Thomas, 1913*b*), and Itabu Creek Head, Corentyne River, Boundary Camp, Guayana (Sanborn, 1941). Two of these bats were netted around the edges of native villages, and one was caught in a net set among blooming cashew trees.

Reproduction. 15 June: 1 male (testes 3 x 2). 5 August: 1 pregnant female (c-r length 14).

Specimens collected (3). Nevati, 1; San Juan, 1 (USNM); San Pablo, 1.

Anoura brevirostrum Carter

This recently described species has been recorded from the type locality (31 km. S Tingo Maria, 850 meters), from 19 km. S Tingo Maria, and from Divisoria en Cordillera Azul, about 600 meters, all in the Departamento de Huánuco (Carter, 1968).

Anoura caudifera (É. Geoffroy St.-Hilaire)

Specimens have been recorded from the *Victoc Valley, near Tarma, Departamento de Junín (Sanborn, 1941), three localities in the Departamento de Cuzco, and from Segrario [Sagraria], Departamento de Puno (Sanborn, 1951*a*). All of these localities are on the eastern slopes of the Andes at elevations of 2000-9000 feet. *A. c. aequatoris* (Lönnberg) is the subspecies reported from Perú.

Anoura geoffroyi Gray

Distribution. Occurs along both sides of Andes where it has been collected at elevations of 1000-9000 feet. Known west of Andes from Huancabamba, Departamento de Piura (San-

born, 1933), south to Provincia de Lima, Departamento de Lima (de la Puente, 1951:11), and east of Andes from Shapaja, Juan Guerra, and Lomas, Departamento de San Martín (Jamet and Vasquez, 1957), south to Ollantaytambo [Ollantaitambo], Departamento de Cuzco (Thomas, 1920*b*).

Remarks. A colony of about 75 of these bats was encountered in a long tunnel at a power plant located 32 km. NE Tarma. Several small clusters were roosting in depressions on the rough earthen and rock ceiling of a room about 30 feet high and 25 feet wide. The room was about 200 feet from the entrance of the tunnel and was completely dark. Of the 51 specimens captured, 17 were females and 34 were males. The area surrounding the tunnel was dry and rocky with no trees nearer than 750 meters where several small varieties grew along the Río Palca. There were, however, many low flowering shrubs on the nearby slopes.

Two *A. geoffroyi* were netted in front of a 12-foot bush covered with yellow flowers, three-fourths of an inch wide, that tapered to narrow bases that were one and three-fourths inches long. The same tree was exceptionally attractive to hummingbirds during the day.

The subspecies recorded from Perú is *A. g. peruana* Tschudi.

Reproduction. 19 June: 1 non-pregnant female. 24 June: 2 pregnant females (c-r length 19, 42), 15 non-pregnant females, 34 males (testes 2 x 1 to 6 x 4, av. 3.3 x 2.1).

Specimens collected (56). San Ramón, 3; Tarma, 53.

Choeroniscus inca (Thomas)

The holotype was collected near the [Río] Yahuarmayo [Yaharamayo], 1200 feet, Departamento de Puno (Thomas, 1912). Two specimens recorded from Los Pozos, Ecuador, two from Kamakuso and Kartabo, British Guiana [Guayana], and nine from Chimanta-tepui, Venezuela (Handley, 1966*a*), indicate a wide distribution for this bat.

Choeroniscus intermedius (J. A. Allen and Chapman)

Distribution. Known only from San Pablo.

Remarks. Two specimens collected at San Pablo evidently are the first to be recorded from other than Trinidad (Goodwin and Greenhall, 1961:248) and extend the known range of this bat approximately 2800 kilometers to the southwest. They were netted in secondary growth around gardens at the edge of virgin evergreen forest.

Reproduction. 12-14 July: 2 non-pregnant females.

Specimens collected (2). San Pablo, 2.

Choeroniscus minor (Peters)

Distribution. Known from Pto. Melandez [Melendez], above Marañón, Departamento de Huánuco, and from San Juan (Handley, 1966*a*).

Remarks. One specimen was netted over a trail in mature evergreen forest.

Reproduction. 26 August: 1 male (juvenile, testes 1.5 x 1).

Specimen collected (1). San Juan, 1 (USNM).

Lichonycteris obscura Thomas

Distribution. Known only from San Juan.

Remarks. A single specimen collected at San Juan is the first Peruvian record for this species. Apparently, the nearest previous records were from the provinces of Darién, San Blas and Bocas del Toro, Panamá (Handley, 1966*b*), and from Surinam (Miller, 1900*a*).

One was netted over a trail in mature evergreen forest near the edge of the village clearing.

Specimen collected (1). San Juan, 1 (USNM).

Carollia castanea H. Allen

Distribution. Known from San Juan, San Pablo, and San Ramón.

Remarks. Seven specimens from Idma, Departamento de Cuzco, recorded as *Hemiderma castaneum* (Thomas, 1920*b*), have been identified by Dr. Charles O. Handley, Jr., as *Carollia subrufa* (see below). Specimens of *C. castanea,* that I collected near San Ramón and at San Juan and San Pablo, and a series reported from *[Puerto] Indiana, Río Amazonas, Departamento de Loreto by Pirlot (1968), are the first authentic records for Perú. According to Thomas, specimens obtained from Ecuador were similar to those from Idma, Perú. There is, therefore, considerable probability that the Ecuadorian specimens mentioned by him also are *Carollia subrufa.* The nearest definite records to Perú of *castanea* that I have been able to locate are from Río Tarra, upper Río Catatumbo, Colombia (Hershkovitz, 1949).

Specimens were netted in a plantation near San Ramón where many bananas and papayas grew, and in Campa Indian gardens and villages where the same and other fruits were present.

Reproduction. 28 June: 2 males (testes 5 x 3, 4 x 2). 19 July: 1 non-pregnant female. 23-24 July: 1 non-pregnant female, 2 males (testes 5 x 3, 5 x 3). 5 August: 1 non-pregnant female. 26 August: 1 male (testes 6 x 4).

Specimens collected (24). San Juan, 19 (9 USNM); San Pablo, 3; San Ramón, 2.

Carollia perspicillata (Linnaeus)

Distribution. Common throughout Amazonas; known from junction of Ríos Amazonas and Nany [Nanay], 16 km. below Iquitos, Departamento de Loreto (AMNH 130178-130185), south to *San Juan, Provincia de Sandia, Departamento de Puno (Sanborn, 1953).

Remarks. Colonies of 10-25 individuals were encountered, either in compact clusters or loosely associated in hollow trees and logs, buildings, and cement drains. These bats frequently occupied roosts with *Glossophaga soricina, Phyllostomus elongatus,* or *Saccopteryx bilineata,* and once were found roosting with *Micronycteris hirsuta.* At San Pablo, individuals entered our thatched Campa Indian hut each night to eat bananas. Before we began covering bananas, we lost up to two pounds per night. At Nevati, I caught several in rat traps, baited with banana, that were set on the ground around the periphery of the village. *C. p. perspicillata* (Linnaeus) is the subspecies reported from Perú.

Reproduction. 15-17 June: 10 non-pregnant females, 10 males (testes 3 x 2 to 7 x 5, av. 5.3 x 3.5). 26-28 June: 2 non-pregnant females. 3-7 July: 6 non-pregnant females, 5 males (testes 7 x 4, 6 x 4, 5 x 4, 3 x 2, 3 x 2). 22-26 July: 1 non-pregnant female, 2 males (testes 9 x 7, 6 x 4). 10 August: 7 non-pregnant females, 6 males (testes 8 x 6, 7 x 5, 6 x 4, 6 x 4, 6 x 4, 3 x 1). 12-13 August: 2 non-pregnant females, 2 males (testes 8 x 6, 7 x 5). 18 August: 2 non-pregnant females, 6 males (testes 9 x 5, 8 x 4, 6 x 5, 6 x 4, 3 x 2, 2.5 x 1). 26 August: 2 pregnant females (c-r length 24, 23). 27 August: 1 pregnant female (c-r length 5); 1 non-pregnant female.

Specimens collected (319). Nevati, 62; San Juan, 185; San Pablo, 60; San Ramón, 12.

Carollia subrufa (Hahn)

Seven specimens that were erroneously reported as *Hemiderma castaneum* from Idma, 6000 feet, Departamento de Cuzco (Thomas, 1920*b*), provide the only record from Perú, but collections probably contain other specimens that are misidentified as *C. perspicillata.* I am indebted to C. O. Handley, Jr., for the correct identification of the specimens from Idma.

Rhinophylla pumilio Peters

Distribution. Known from the following localities: Yurac Yacu, about 2500 feet, a little more than 32 km. WNW Mayobamba, Departamento de San Martín (Thomas, 1927*a*); *Puerto Indiano [Indiana], Río Amazonas, and 33 mi. SE Pucallpa, and Loreto, all three in Departamento de Loreto (Carter, 1966); San Juan; San Pablo.

Remarks. This bat was netted especially in Indian gardens where bananas and papayas were grown and over trails deep within mature evergreen forest. A male was captured in a banana-baited rat trap set on the ground beneath ferns in dense mature forest about a kilometer from San Pablo.

Reproduction. 16 June: 4 non-pregnant females, 1 male (testes 4 x 3). 3 July: 1 male (testes 6 x 4). 6-8 July: 2 non-pregnant females, 1 male (testes 5 x 4). 11-14 July: 2 non-pregnant females, 3 males (testes 4 x 3, 2 x 2, 2 x 1.5). 16 July: 1 non-pregnant female, 1 male (testes 5 x 3). 5 August: 1 non-pregnant female, 1 male (testes 5 x 3.5).

Specimens collected (25). Nevati, 5; San Juan, 6 (4 USNM); San Pablo, 14.

Rhinophylla fischerae Carter

Distribution. Known from Pucallpa and from 98 km. SE Pucallpa, about 585 feet, Departamento de Loreto (Carter, 1966), and from San Juan and San Pablo.

Remarks. This bat is easily distinguished in the field from *R. pumilio* by the long fur, which covers and overlaps its interfemoral membrane along the rump. In *R. pumilio,* the entire membrane is bare and never overlapped by long fur. *R. fischerae* was caught in the same nets with *R. pumilio.* The two were most often taken in or near gardens where bananas and papayas were grown.

Reproduction. 2 July: 1 male (testes 5 x 4). 7-8 July: 6 non-pregnant females, 3 males (testes 5 x 4, 5 x 4, 2 x 1). 13 July: 1 non-pregnant female. 22 July: 1 non-pregnant female. 25 July: 1 male (testes 6 x 5). 5 August: 1 non-pregnant female.

Specimens collected (26). San Juan, 14 (7 USNM); San Pablo, 12.

Sturnira bidens (Thomas)

This bat has been reported only from the type locality in Ecuador (Thomas, 1915) and from humid montane forest on the eastern slope of the Cordillera Carpish along the Carretera Central, between Huánuco and Tingo Maria, Departamento de Huánuco (Gardner and O'Neill, 1969).

Sturnira erythromos (Tschudi)

Distribution. Known from east slope of Cordillera Carpish along Carretera Central, between Huánuco and Tingo Maria, Departamento de Huánuco (Gardner and O'Neill, 1969), and from near Tarma, south to *Limacpunco, near Marcapata (FMNH 75182-75185), and Machu Picchu (Gardner and O'Neill, 1969), both in Departamento de Cuzco.

Remarks. Our specimens from near Tarma appear to represent the same species that was described by Tschudi (1844:64). He recorded it as occurring between latitudes 12 and 14° S.

In the field this bat is distinguishable from *S. ludovici* (forearm 42.6-48.0) and *S. tildae* (forearm 45.0-48.0) by its smaller size (forearm 38.0-41.3), and from *S. lilium* in that the lingual sides of the lower molars are without prominent cusps, leaving a nearly continuous edge (*lilium* has prominent cusps along the inner margin of the lower molars). For comparisons of *S. bidens* and *S. erythromos*, see Gardner and O'Neill (1969).

These small bats were netted in a deep, narrow valley along a stream in a brushy forest (10-35 feet tall).

Reproduction. 19 June: 2 non-pregnant females (juveniles), 1 male (testes 5 x 3). 24 June: 1 male (testes 7 x 4).

Specimens collected (7). Tarma, 7.

Sturnira lilium (É. Geoffroy St.-Hilaire)

Distribution. Probably common throughout Amazonas; known from [Río] Huallaga (no exact locality, departamento not specified—Dobson, 1878:538-540), south to [Puerto] Maldonado, Río Madre de Dios, Departamento de Madre de Dios (FMNH 84397-84399), and Ocabamba (Thomas, 1920*b*), and *Quincemil, Huajyumbe [Río Huajllumbe], Provincia de Quispicanchi (FMNH 84400-84401), both in Departamento de Cuzco.

Remarks. The scarcity of records for this bat in Perú is probably due to the fact that most earlier collectors did not have mist nets and were forced to rely on finding roosts. All specimens that we collected were netted near wild fig, banana, papaya, and other fruit trees. The subspecies reported from Perú is *S. l. lilium* (Geoffroy).

Reproduction. 28-29 June: 8 non-pregnant females, 10 males (testes 2 x 1 to 7 x 6, av. 4.3 x 3.1). 4-6 July: 4 males (testes 6 x 4, 6 x 4, 5 x 4, 4 x 3). 8-9 July: 1 non-pregnant female, 1 male (testes 5 x 4). 11-13 July: 1 non-pregnant female, 6 males (testes 6 x 4, 6 x 3, 5 x 4, 3 x 3, 3 x 2, 3 x 2). 24-26 July: 1 pregnant female (c-r length 13), 4 non-pregnant females. 30 July: 2 non-pregnant females, 2 males (testes 6 x 5, 5 x 4). 4 August: 1 male (testes 5 x 3). 24 August: 1 pregnant female (c-r length 12).

Specimens collected (81). Nevati, 10; San Juan, 22 (7 USNM); San Pablo, 21; San Ramón, 28.

Sturnira ludovici Anthony

Distribution. Known from Amacho, near Marcapata, Departamento de Cuzco (FMNH 75186-75189), and from near Tarma, San Ramón, and Nevati.

Remarks. Specimens were netted at elevations of 900-7300 feet, especially near fruit trees. The subspecies reported from Perú is *S. l. ludovici* Anthony.

Reproduction. 19 June: 1 male (testes 5 x 3). 28-29 June: 1 non-pregnant female, 1 male (testes 3 x 1). 12 July: 1 male (testes 3 x 2).

Specimens collected (9). Nevati, 1; San Ramón, 7; Tarma, 1.

Sturnira magna de la Torre

Distribution. Known from the type locality at Santa Cecilia, about 350 feet, Río Manití, near Iquitos, Departamento de Loreto (de la Torre, 1966), and from San Juan and San Pablo.

Remarks. This bat is easily distinguished from all other members of the genus, known to occur east of the Andes, by its large size (forearm 56.4-59.3). Forearms of the other Amazonian species of *Sturnira* measure less than 49 (usually not more than 47).

One specimen was taken in a net set across a narrow trail leading from San Pablo to a garden where bananas and papayas were grown. The trail was completely enclosed by dense

vines and was 6 feet wide and 7-10 feet high. Another was taken in a similar garden, and a third was netted at the edge of a large area of newly cut trees surrounded by mature forest.

Reproduction. 7 July: 1 male (testes 6 x 4). 12 July: 1 male (testes 7 x 5). 25 July: 1 male (testes 6 x 4).

Specimens collected (3). San Juan, 1; San Pablo, 2.

Sturnira tildae de la Torre

Distribution. Known from *Shahuayo, Provincia de Coronel Portillo, Departamento de Loreto, and from Nevati, San Juan, and San Pablo.

Remarks. This bat was described from Trinidad and recently recorded for the first time on the mainland of South America from Guayana (Hill, 1964). The known range of this bat is now extended across the continent to Perú.

Individuals were netted in gardens where bananas and papayas were grown and at the edge of a freshly cut area in mature evergreen forest.

Reproduction. 7-12 July: 2 non-pregnant females, 1 male (testes 7 x 5).

Specimens collected (6). Nevati, 2; San Juan, 2 (USNM); Shahuayo, 1.

Uroderma bilobatum Peters

Distribution. Recorded west of Andes from *Matapalo, Departamento de Tumbes (FMNH 81069-81078) and east of Andes from *Puerto Indiana, Río Amazonas, Departamento de Loreto (Davis, 1968), south to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*). Ranges from lowland Amazonas to at least 6000 feet in Andes.

Remarks. Tent-making bats were netted in secondary growth around the periphery of villages and at the edge of a freshly cleared area in mature forest. *U. b. thomasi* Andersen is the subspecies reported from Perú.

Reproduction. 7 July: 1 male (testes 5 x 3). 14 July: 1 male (testes 7 x 5). 5 August: 1 pregnant female (c-r length 7), 1 male (testes 5 x 4). 12-13 August: 2 non-pregnant females.

Specimens collected (8). Nevati, 1; San Juan, 5 (4 USNM); San Pablo, 2.

Uroderma magnirostrum Davis

This species probably occurs throughout the Peruvian Amazonas. It has been reported from the mouth of the Río Mazán, from Sarayacu, Río Ucayali, and from Balta, Río Curanja, all in Departamento de Loreto (Davis, 1968).

Vampyrops dorsalis Thomas

Thomas' broad-nosed bat has been recorded from *Comante, 6500 feet (Sanborn, 1955), and from Marcapata (Sanborn, 1951*a*), both in the Departamento de Cuzco.

Vampyrops lineatus (É. Geoffroy St.-Hilaire)

Apparently, this bat was erroneously recorded from west of the Andes at Guayabamba, 6000 feet, Departamento de La Libertad, by J. A. Allen (1897). According to Goodwin (1953:259), the specimens in question actually originated at *Santa Rosa de Huayabamba, 6000 feet, Departamento de San Martín, on the eastern slope of the Andes. *V. lineatus* has not been reported from elsewhere in Perú.

Vampyrops vittatus (Peters)

Distribution. Recorded west of Andes from *Gruta de Niñabamba, *Hacienda Niñabamba, Provincia Hualgayoc, Departamento de Cajamarca (Peters, 1880 and Sanborn, 1955), and east of Andes from *Victoc Valley, near Tarma, Departamento de Junín, south to region near Marcapata, Departamento de Cuzco (Sanborn, 1955). For the use of *V. vittatus* in place of *V. fumosus* and *V. infuscus* see Sanborn (1955).

Remarks. Near San Ramón *V. vittatus* was netted beneath fruiting wild fig trees that were as much as 100 feet tall. Many large bats were observed near these trees; several *vittatus* were netted 600 feet from the nearest visible fig tree, while carrying partly eaten figs 30 mm in diameter. Near San Juan a compact cluster of about 20 individuals was found on the ceiling of a large but shallow cave in mature forest. The cave was wet inside and a stream flowed from its entrance. A single pistol shot of .22 dust killed nine females. Other bats shot in the same cave were *Phyllostomus hastatus* and *Peropteryx kappleri*.

Reproduction. 27-28 June: 4 non-pregnant females, 3 males (testes 6 x 4, 6 x 4, 4 x 3). 16 August: 9 non-pregnant females.

Specimens collected (17). San Juan, 9 (USNM); San Ramón, 8.

Vampyrops helleri Peters

Distribution. Recorded west of Andes from *Matapalo, Departamento de Tumbes (Sanborn, 1955), and east of Andes from Pebas, Río Amazonas (Thomas, 1928*c*), and from Pucallpa, Río Ucayali, both in Departamento de Loreto (Sanborn, 1949*b*).

Remarks. Specimens collected in 1964 extend the known range to San Juan, and to Río Seco, 2400 feet, near San Ramón, Departamento de Junín. They were netted at the edge of a newly cut area in mature forest and in secondary growth consisting of dense, low brush and vines. For use of *V. helleri* in place of *V. zarhinus* see Sanborn (1955).

Reproduction. 25 June: 1 male (testes 2 x 1). 29 July: 1 pregnant female (c-r length 22). 5 August: 2 pregnant females (c-r lengths 8, 27), 2 non-pregnant females, 1 male (testes 7 x 5). 12-13 August: 2 males (testes 4 x 3, 3 x 2).

Specimens collected (14). San Juan, 13 (10 USNM); San Ramón (Río Seco), 1.

Vampyrodes caraccioloi Thomas

Distribution. Known in Amazonas from San Lorenzo, 500 feet, Río Marañón, about opposite mouth of Río Huallaga, and from Masisea, 1000 feet, Río Ucayali, both in Departamento de Loreto (Thomas, 1924), south to San Juan and San Ramón.

Remarks. Great striped-faced bats were netted over a narrow roadway among banana plants about 100 feet from several large wild fig trees laden with ripe fruit, and over a tractor trail near a large field of ripening papayas. None of these bats was netted in the San Ramón area except near these food sources. At San Pablo one was netted over a trail leading to a garden where there were many ripe papayas. *V. c. ornatus* Thomas (type locality, San Lorenzo) is the subspecies reported from Perú.

Reproduction. 27-29 June: 2 non-pregnant females, 4 males (testes 6 x 5, 6 x 4.5, 5 x 4, 4 x 3). 7 July: 1 pregnant female (c-r length 17).

Specimens collected (7). San Pablo, 1; San Ramón, 6.

Vampyressa bidens (Dobson)

This bat is known from the Río Mazan, N of Iquitos (AMNH 98780); San Lorenzo, 500 feet, Río Marañón; and from Tushemo [Tushma], 5 km. SW of Masisea, Río Ucayali, all in Departamento de Loreto (Sanborn, 1936). It has been reported also from the [Río] Huallaga (no exact locality, departamento not specified—Dobson, 1878:535-536). For classification of *Vampyriscus* as a subgenus of *Vampyressa,* see Peterson (1968).

Vampyressa melissa Thomas

The holotype was collected at Puca Tambo, 7100 feet, ESE of Chachapoyas, Departamento de Amazonas (Thomas, 1926*a*); no additional specimens have been reported.

Vampyressa pusilla (Wagner)

Little yellow-eared bats occur throughout the Amazonas. They have been recorded from San Lorenzo, 500 feet, Río Marañón, Departamento de Loreto (Thomas, 1924), to *Hacienda Cadena, near Marcapata, Departamento de Cuzco (Sanborn, 1953). *V. p. thyone* Thomas is the subspecies reported from Perú. See Goodwin (1963) for a discussion of the subspecies of *V. pusilla.*

Chiroderma trinitatum Goodwin

Distribution. Known from *Mirim, about 600 feet, *Quebrada Esperanza, Río Yavari (FMNH 89083, 89085), and *Boca Río Yaquerana, about 600 feet, *Alto Río Yavari (FMNH 89093), both localities in Departamento de Loreto, and from San Pablo.

Remarks. Three specimens from the Departamento de Loreto and one from San Pablo are the first to be reported from Perú. The only previous records are from Darién, Panamá (Handley, 1966), and Cumaca, Trinidad (Goodwin and Greenhall, 1961:258). The Peruvian specimens do not differ significantly from Trinidadian specimens with which they were compared. The lesser white-lined bat netted at San Pablo was taken in secondary vegetation at the edge of a small garden where bananas and papayas were grown.

Reproduction. 21 July: 1 non-pregnant female.

Specimen collected (1). San Pablo, 1.

Chiroderma villosum Peters

Distribution. Known from *Quistococha, near Iquitos (USNM 337940), San Lorenzo, Río Marañón (Thomas, 1927*a*), and Masisea, Río Ucayali (Thomas, 1928*b*), all three localities in Departamento de Loreto, and from San Juan.

Remarks. A single specimen was netted at San Juan over a trail in dense mature forest near a stream. The Peruvian subspecies is probably *C. v. villosum* Peters, which has been reported from Brazil to Venezuela. *C. v. jesupi* J. A. Allen is known from northern Colombia to southern Mexico (see Handley, 1960).

Reproduction. 13 August: 1 non-pregnant female.

Specimen collected (1). San Juan, 1 (USNM).

Ectophylla macconnelli (Thomas)

Distribution. Occurs throughout Amazonas; known from Santa Cecilia, Río Manití, near Iquitos, Departamento de Loreto (FMNH 87085-87096), to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Remarks. One female was netted at the edge of a small freshly cut clearing in dense mature forest.

Reproduction. 2 August: 1 pregnant female (c-r length 14).

Specimen collected (1). San Juan, 1 (USNM).

Artibeus cinereus (Gervais)

Distribution. Recorded from Chanchamayo about 3000 feet, Departamento de Junín (Thomas, 1893), *Cerro Azul 2000 feet, near Contamana, 32 km. E Río Ucayali (Thomas, 1928*b*), and from Tushemo [Tushma], 1000 feet, near Masisea, Río Ucayali, both in Departamento de Loreto (Thomas, 1924). There is another record "Brazil (Rio Ucayali)" (Dobson, 1878:520-521), which undoubtedly refers to the Río Ucayali, Departamento de Loreto, Perú.

I have been unable to examine two specimens from *[Puerto] Indiana, Río Amazonas, Departamento de Loreto, that were reported by Pirlot (1968) as *Artibeus nanus* Andersen, but I suspect that they represent *A. cinereus*.

Remarks. These small fruit bats were netted at San Juan along the edge of a freshly cut area in mature forest. The subspecies *A. c. glaucus* Thomas has been reported from an elevation of about 3000 feet in the Departamento de Junín (the type locality), whereas *A. c. pumilio* Thomas has been reported from the Amazonas region.

Reproduction. 25 July: 1 non-pregnant female. 5 August: 1 male (testes 4 x 3).

Specimens collected (9). San Juan, 9 (4 USNM).

Artibeus jamaicensis Leach

Distribution. Probably common throughout Amazonas. Known west of Andes from *Matapalo, Departamento de Tumbes (FMNH 81060-81061, 81063, 81066-81067), and Canchaque, Departamento de Piura (FMNH 81139), south to *Hacienda Carmen, near Motupe, Departamento de Lambayeque (FMNH 81127-81128, 81130-81136, 81138). Recorded previously east of Andes from northern and central Amazonas as follows (records from north to south): Pebas, Departamento de Loreto (Thomas, 1928*c*); about 32 km. WNW Moyobamba, Departamento de San Martín (Thomas, 1927*a*); Contamana, 500 feet, Río Ucayali (Thomas, 1928*b*), and Pucallpa, Río Ucayali, both in Departamento de Loreto; Agua Caliente, Río Pachitea, Departamento de Huánuco (Sanborn, 1949*b*).

Remarks. Specimens of the Jamaican fruit-eating bat were netted in virtually all habitats studied, but abundance in any given area seemed to be related to the amount of ripe fruit available. *A. jamaicensis* was commonly taken, for example, near papayas with ripe fruits and near fruiting wild figs at San Ramón, but individuals were netted only occasionally in virgin forest away from such food supplies. One female was netted while carrying a wild fig (about 30 mm in diameter). The status of Peruvian populations of the Jamaican fruit-eating bat is open to question.

Peruvian species of the genus *Artibeus* are widely distributed in the eastern Amazonas, and four species may be netted at a single site at San Juan. These species are easily identifiable in the field, but misidentifications have resulted from the fact that only three instead of four species have been recognized (two distinct species have been identified as *Artibeus jamaicensis*, both of which occur at San Juan and are easily distinguishable). The characters presented in Table 4 will serve to differentiate the four species of *Artibeus* that inhabit the Amazonas. Measurements for two randomly selected skulls (male and female) of the unrecognized species, followed in parenthesis by those of an adult female of *A. jamaicensis* are: greatest length, 28.0,

Table 4. External characteristics of Peruvian bats of the genus *Artibeus* from east of the Andes.

Characteristics	*A. lituratus*	*A. jamaicensis*	*A.* species	*A. cinereus*
Forearm length	74.3-74.8	68.6-71.1	58.3-60.1	35.2-37.3
Dorsal fur length	6-8	5-7	8-11	5-7
Eye stripes	distinct	faint	usually absent	distinct to faint
Tragus color	yellow tipped	entirely brown	dark brown to black	yellow
Dorsum color	pale reddish brown	medium grayish brown	dark brown to black	pale reddish or grayish brown
Shoulder color	paler than dorsum	much paler than dorsum	about same as dorsum	may be paler than dorsum

27.5 (31.7); depth of brain case, 10.8, 10.6 (11.5); zygomatic breadth, 17.3, 16.9 (19.6); breadth of brain case, 12.5, 12.1 (13.8); interorbital breadth, 6.9, 6.3 (7.7); length of maxillary toothrow, 10.2, 9.9 (12.0); palatal breadth, 12.9, 12.5 (14.9); postpalatal length, 8.4, 8.5 (9.7).

The smaller of the two species currently classified as *A. jamaicensis* has not been recognized in previous literature pertaining to Perú, but collections undoubtedly contain additional specimens. We collected this long furred, nearly black *Artibeus* only at San Juan, but it probably ranges widely in hilly areas bordering the eastern slopes of the Andes. Individuals of this bat were netted over trails and over a stream in mature evergeen forest. None was netted around fruit trees in Indian gardens where *A. jamaicensis* was taken much more frequently than in the forest. Eight specimens (5 USNM), not listed below, were collected at San Juan, and the following reproductive data were recorded—25 July-2 August: 3 males (testes 8 x 6, 8 x 5, 6 x 4). 16 August: 1 non-pregnant female. 26 August: 1 pregnant female (c-r length 9).

Reproduction. 28 June: 14 non-pregnant females, 15 males (testes 3 x 2 to 10 x 7, av. 5.9 x 3.8). 6 July: 2 non-pregnant females. 11-15 July: 2 non-pregnant females, 2 males (testes 8 x 7, 8 x 6). 20-21 July: 2 males (testes 7 x 5, 4 x 3). 13 August: 3 non-pregnant females.

Specimens collected (54). Nevati, 4; San Juan, 5 (USNM); San Pablo, 8; San Ramón, 37.

Artibeus lituratus (Olfers)

Distribution. Presently known only from northern and central Amazonas but probably occurring throughout most of eastern Perú. Recorded from Yurac Yacu, about 32 km. WNW Moyobamba (Thomas, 1927*a*) and from Moyobamba (Osgood, 1914), Departamento de San Martín, southward to Agua Caliente, Río Pachitea, Departamento de Huánuco, and Pucallpa, Río Ucayali, Departamento de Loreto (Sanborn, 1949*b*).

Remarks. Big fruit-eating bats were most often netted around fruit trees in the villages. Several were netted at San Juan over a stream in mature forest. Eastern Perú is the type locality for *A. l. hercules* Rehn, but Cabrera (1957:90) has suggested that this region might be an area of intergradation between *hercules* and *A. l. lituratus* (Olfers).

Reproduction. 4 July: 1 non-pregnant female, 1 male (testes 6 x 4). 18 July: 1 male (testes 10 x 8). 23 July: 1 male (testes 6 x 5). 26 July: 1 non-pregnant female, 1 male (testes 6 x 3).

Specimens collected (17). Nevati, 2; San Juan, 10 (8 USNM); San Pablo, 5.

Sphaeronycteris toxophyllum Peters

A single specimen was taken at Pebas, Río Amazonas, Departamento de Loreto (Rehn, 1900). The type locality of this bat was later restricted to Pebas by Cabrera (1957:92).

Family **DESMODONTIDAE**

Desmodus rotundus (É. Geoffroy St.-Hilaire)

Distribution. Most widely distributed of all Peruvian bats; recorded from at least 12 departments in and on both sides of Andes throughout entire length of Perú (de la Puente,

1951:18-19). Known from sea level on Isla de Asia (USNM 236911-236914) to elevations up to at least 11,000 feet in Andes (Thomas, 1927*b*).

Remarks. Large series of vampire bats were not collected because we intentionally avoided setting nets near live stock and in other situations where considerable numbers might have been taken. Vampires were common in villages, where they fed on both animals and Indians. One Campa Indian boy, about four years old, showed evidence of 14 recent bites on the top of his head where the hair had been cut short. Our observations, combined with statements of local Indians, suggested that vampires have definite preferences for one victim over another. Apparently, these bats repeatedly will seek out a single individual while bypassing those sleeping near him in the same hut. Similar observations have been made on Trinidad (Goodwin and Greenhall, 1961:268-269). The subspecies, *D. r. rotundus,* has been recorded from both sides of the Andes in Perú.

Reproduction. 28 June: 3 males (testes 7 x 4, 7 x 4, 6 x 4). 3 July: 1 non-pregnant female, 1 male (testes 7 x 5). 8 July: 1 male (testes 7 x 4). 25 July: 1 male (testes 5 x 3).

Specimens collected (10). Nevati, 2; San Juan, 1; San Pablo, 5; San Ramón, 2.

Diaemus youngi (Jentink)

This vampire bat has been reported from Pebas, 300 feet, Río Amazonas (Thomas, 1928*c*), and from Yarinacocha, Río Ucayali (Sanborn, 1949*b*), both localities in Departamento de Loreto. *D. y. cypselinus* Thomas is the subspecies on record from Perú (see Husson, 1962:198).

Diphylla ecaudata Spix

Distribution. Recorded from Puca Tambo, 5100 feet (Thomas, 1926*a*), and Corosha, 8000 feet (Thomas, 1926*b*), both in Departamento de Amazonas, Yurac Yacu, Departamento de San Martín (Thomas, 1927*a*), Yarinacocha, Departamento de Loreto (Sanborn, 1949*b*), and Tushemo [Tushma], near Masisea, Departamento de Pasco (Thomas, 1928*b*).

Remarks. A single specimen was netted adjacent to a place where chickens roosted at Nevati.

Specimen collected (1). Nevati, 1.

Family **FURIPTERIDAE**

Amorphochilus schnablii Peters

A. s. schnablii has been recorded west of the Andes from Tumbes (Peters, 1877) and Zorritos (de la Puente, 1951:22), both in Departamento de Tumbes, south to the Vitor and Tambo valleys, Departamento de Arequipa (Sanborn, 1941), and *A. s. osgoodi* J. A. Allen has been recorded east of the Andes from Balsas, 3000 feet, Departamento de Amazonas (J. A. Allen, 1914).

Furipterus horrens (F. Cuvier)

A single specimen of Cuvier's smoky bat (AMNH 98731), labeled "Peru: Rio Disqui, Ucayali," is the first to be reported for the country. The Río Disqui is not shown on the American Geographical Society Map but it is assumed to be a small tributary of the well-known Río Ucayali, Departamento de Loreto. Previous records of *F. horrens* nearest Perú are from Andagada, Colombia (J. A. Allen, 1916), the Guianas (Sanborn, 1941), and Santa Catarina, Brazil (Vieira, 1942:385-386).

Family **THYROPTERIDAE**

Thyroptera discifera Lichtenstein and Peters

Specimens of this species have been recorded from Iquitos, 400 feet, Río Amazonas (Thomas, 1928*c*), and from Cumeria [Cumaria], 1000 feet, about 10° S, Río Ucayali (Thomas, 1928*b*), both in Departamento de Loreto. *T. d. major* Miller is the only subspecies known from South America.

Thyroptera tricolor Spix

Distribution. Probably occurs throughout Amazonas. First recorded from Marcapata, Departamento de Cuzco (Sanborn, 1951*b*), and now from San Juan.

Remarks. At 5:45 p.m. on 27 August, many small bats were seen flying among the tree tops in dense evergreen forest near San Juan. At 6:15 p.m. a single low-flying *T. tricolor*

struck one of the 10 five-meter nets set about every 200 feet along a trail in the forest. The only other bats taken in these nets were two *Carollia perspicillata*, but rain terminated netting at 7:00 p.m. The subspecies reported from Perú is *T. t. tricolor* Spix; however Cabrera (1957:98) stated that *T. t. albiventer* (Tomes) was probably the correct name for the Peruvian race, although both subspecies could occur in the country.

Specimen collected (1). San Juan, 1 (USNM).

Family **VESPERTILIONIDAE**

Myotis albescens (É. Geoffroy St.-Hilaire)

Distribution. Occurs throughout Amazonas; recorded from *Puerto Indiana, near Pebas, Río Amazonas, Departamento de Loreto (Miller and Allen, 1928:200-203), south to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Remarks. Bats of this species were most often netted near the thatched huts of Indians where they probably roosted. Many were purchased from the Indians.

Reproduction. 18 August: 10 pregnant females (c-r length 8-25, av. 15.3), 13 non-pregnant females, 3 males (testes 8 x 6, 8 x 6, 5 x 4).

Specimens collected (49). Nevati, 7; San Juan, 42 (39 USNM).

Myotis chiloensis (Waterhouse)

Little brown bats have been recorded commonly east of the Andes from Chachapoyas, 7600 feet, Departamento de Amazonas, south to the Río Inambiri [Inambari], Provincia de Carabaya, Departamento de Puno (Miller and Allen, 1928:193-194). West of the Andes, they have been recorded from the Provinces of Celendín and Cutervo, Departamento de Cajamarca, south to Lima, Departamento de Lima (de la Puente, 1951:25). This species has been reported from elevations of about 1000 up to 10,500 feet. *M. c. oxyotis* (Peters) has been recorded throughout most of the Peruvian Andes, and *M. c. atacamensis* (Lataste) is the subspecies reported from the arid and semiarid regions of extreme southen Perú.

Myotis nigricans (Schinz)

Distribution. Recorded at many localities east of Andes from Moyobamba, Departamento de San Martín (Osgood, 1914), south to *Inca Mines (lat. 13° 30′ S, long. 70° W), 6000 feet (J. A. Allen, 1914; Cabrera, 1957:100-101), and Provincia de Sandia (Sanborn, 1953), both in Departamento de Puno. Recorded west of Andes from Provincia de Lima, Departamento de Lima (de la Puente, 1951:28) and from Tambo Valley, Departamento de Arequipa (Sanborn, 1941).

Remarks. I netted *M. nigricans* over streams and especially around palm-thatched Indian huts. Probably they roosted in the thatching. *M. n. nigricans* (Schinz) has been recorded (Sanborn, 1949*b*) east of the Andes in the Amazonas region, and *M. n. nicholsoni* Sanborn has been recorded (Sanborn, 1941) west of the Andes in the arid coastal region.

Reproduction. 13-17 June: 2 pregnant females (c-r length 20, 12), 3 non-pregnant females (1 juv.). 8 July: 1 male (testes 3 x 2). 15 July: 1 male (testes 5 x 3).

Specimens collected (20). Nevati, 12; San Juan, 4; San Pablo, 3; San Ramón, 1.

Myotis simus Thomas

Distribution. Recorded previously from *Apayacu, and Orosa, Río Amazonas (Handley, 1960), Yurimaguas, Río Huallaga (Osgood, 1914), Sarayacu (Thomas, 1901), and Yarinacocha (Sanborn, 1949*b*), Río Ucayali (for additional records on Río Ucayali see Handley, 1960), all in Departamento de Loreto.

Remarks. Three individuals were netted over a small stream near its junction with the Río Azupizu. The Peruvian subspecies is *M. s. simus* Thomas (type locality at Sarayacu).

Reproduction. 10 August: 2 non-pregnant females.

Specimens collected (4). San Juan, 3 (2 USNM); San Pablo, 1.

Eptesicus andinus J. A. Allen

The Andean big brown bat has been recorded along the eastern slopes of the Andes from Vista Alegre, Río Chinchao, Departamento de Huánuco, and from *Maraynioc, 73 km. NE Tarma, 12,000 feet, Departamento de Junín (Davis, 1966). For a complete review of the South American species of *Eptesicus*, see Davis (1966).

Eptesicus brasiliensis (Desmarest)

Distribution. Recorded from *Montealagre and *Puerto Indiana, Río Amazonas, Departamento de Loreto, and from Bellavista, Departamento de Cajamarca (Davis, 1966). Now known also from Nevati and San Juan.

Remarks. One male was netted at the edge of a newly cut clearing in mature forest near San Juan, and another was netted among blooming cashew trees at Nevati. A juvenile, still unable to fly, was captured in a thatched hut in Nevati. Selected measurements (see Davis, 1966) of a male from Nevati are: length of maxillary toothrow, 6.1; third metacarpal, 40.5; forearm, 41.9; dorsal fur between the shoulders, 6-8 (preserved in alcohol). The Peruvian subspecies is *E. b. thomasi* Davis.

Reproduction. 13-17 June: 1 juv. 5 August: 1 male (testes 8 x 5).

Specimens collected (3). Nevati, 2; San Juan, 1 (USNM).

Eptesicus innoxius (Gervais)

This monotypic species has been collected from sea level to about 3000 feet along the arid coastal belt west of the Andes. The type locality is Amotape, Departamento de Piura. Specimens have been reported from Piura, 150 feet, Departamento de Piura, south to Puerto Eten, Departamento de Lambayeque (Davis, 1966).

Eptesicus montosus Thomas

Distribution. Peruvian records limited to region between San Ramón and Tarma, about 3000 feet, *Valle de Chanchamayo, Departamento de Junín (Thomas, 1893; 1920*a*).

Remarks. Thomas (1893) listed the locality in Chanchamayo as: "Chanchamayo, near Tarma, approximately in lat. 11° 20′ S, and long. 75° 40′ E," and reported that the "altitude of Chanchamayo is about 3000 feet." The Chanchamayo Valley is not shown on the maps available to me. This valley is, however, a well-known collecting site on the east side of the Andes in Central Perú; San Ramón and Tarma, where I collected mammals, are located therein. Thomas (1920*a*) described *Eptesicus inca* and designated "Chanchamayo, Cuzco, Peru," as its type locality. If there is a place named Chanchamayo in the Departamento de Cuzco it is unknown to the Peruvian Government. Mr. Philip Hershkovitz, Field Museum of Natural History (personal communication), who has made a thorough study of Peruvian collecting localities, believes that the *Eptesicus* labeled "Chanchamayo, Cuzco, Peru" were undoubtedly collected in Valle de Chanchamayo, Departamento de Junín, at the same place that was described by Thomas in 1893.

Comparison of Thomas' (1893, 1920*a*) papers indicates that the specimen reported as "*Vesperus fuscus* Palisot de Beauvois" in 1893 may have been the holotype of *Eptesicus inca* Thomas (=*E. montosus* Thomas), described in 1920. Davis (1966) listed no specimens of the genus *Eptesicus* from near Tarma.

A female was netted over a small stream in evergreen forest at the edge of a large plantation near San Ramón. Selected measurements for this specimen are: length of maxillary toothrow, 5.8; third metacarpal, 39.7; forearm, 42.6; dorsal fur from between the shoulders, 8-11 (preserved in alcohol). The Peruvian subspecies is *E. m. chiralensis* Anthony.

Specimen collected (1). San Ramón, 1.

Histiotus macrotus (Pöppig)

This bat is known in the western slopes of the Andes from Hacienda Chucarapi, Valle de Tambo, Departamento de Arequipa, and in the Andes east of the Central Cordillera from near the south end of Lake Titicaca, Yunguyo, Departamento de Puno (Sanborn, 1941), and from Lircay, Departamento de Huancavelica (FMNH 75149). *H. m. laephotis* Thomas is the subspecies reported from Perú.

Histiotus montanus (Philippi and Landbeck)

Big-eared brown bats have been recorded from Marcapata, Departamento de Cuzco (Sanborn, 1951*a*), and from Segrario [Sagraria], 70° 15′ W, 13° 55′ S, 2200 feet, Departamento de Puno (Anthony, 1920; Sanborn, 1951*a*). There are also records from "Hausampilla, Peru (9,000 feet)" and "East coast of Peru" published by Dobson (1878: 189-190). Hausampilla is not shown on Peruvian maps; the specimen from the "East coast" probably came from somewhere along the eastern slope of the Andes. The subspecies recorded from Perú is *H. m. inambarus* (Anthony).

Lasiurus borealis (Müller)

Red bats have been recorded east of the Andes from Condechaca, 7000 feet, Departamento de Amazonas (Thomas, 1926*a*), southward to Marcapata, Departamento de Cuzco (Sanborn, 1951*a*), and the *Inca Mines, near Juliaca, Departamento de Puno (J. A. Allen, 1901). West of the Andes red bats have been recorded from Lima and Callao, Departamento de Lima (de la Puente, 1951:29-30). *L. b. bonariensis* (Lesson and Garnat) is the subspecies that was reported as occurring both east and west of the Andes by de la Puente (1951:30); however Handley (1960) classified the specimen from Juliaca as *L. b. frantzii* Peters, and Cabrera (1957:113) listed *L. b. varius* (Pöppig) as occurring in southern Perú. Andean races of *Lasiurus* are poorly known.

Pirlot (1968) reported a juvenile as "*Dasypterus* sp." from *[Puerto] Indiana, Río Amazonas, Departamento de Loreto. This specimen likely is *L. ega* but could be *L. borealis*.

Lasiurus cinereus (Palisot de Beauvois)

Apparently, the only Peruvian record is a single specimen collected at *Limacpunco, about 7900 feet, near Marcapata, Departamento de Cuzco (Sanborn, 1953). The only recognized subspecies in South America is *L. c. villosissimus* (see Sanborn and Crespo, 1957).

Tomopeas ravus Miller

This monotypic species is known only from the arid coastal belt of Perú where it has been recorded from Monte Grande, 14 km. N, 25 km. E, Talara, Departamento de Piura (Davis, 1970), to Chosica, Departamento de Lima (Miller, 1900*b*). The type locality is *Yayan, about 3080 feet, Departamento de Cajamarca. Davis (1970) has summarized the records of occurrence of this bat.

Family **MOLOSSIDAE**

Molossops brachymeles (Peters)

The holotype was obtained from an unspecified locality in Perú (Peters, 1865), but no additional specimens have been reported from the country.

Molossops milleri Osgood

A single specimen, the holotype, was obtained at Yurimaguas, 600 feet, Río Huallaga, Departamento de Loreto (Osgood, 1914).

Molossops temminckii (Burmeister)

Distribution. Known only from San Juan, but probably occurs elsewhere in eastern Perú.

Remarks. Two specimens collected at San Juan, which provide the first Peruvian records for this bat, were netted along the edge of newly cut mature forest on the south side of the village. About two acres of large trees had been cut only a few hours earlier, and an unusually large number of insects were flying in the area. At dusk, approximately 30-40 small molossids were foraging over the cleared area, but most were flying too high to be netted.

M. t. griseiventer Sanborn has been reported from the Departamento de Tolima, Colombia (Sanborn, 1941). The taxonomic status of Peruvian specimens is uncertain.

Reproduction. 5 August: 2 pregnant females (c-r lengths both 20).

Specimens collected (2). San Juan, 2 (USNM).

Tadarida brasiliensis (I. Geoffroy St.-Hilaire)

Brazilian free-tailed bats occur throughout most of Perú, from near sea level to elevations of at least 6000 feet in the Andes at Machu Picchu, Departamento de Cuzco (Thomas, 1920*b*). The species has been recorded east of the Andes from the Provincia de San Martín, Departamento de San Martín (Jamet and Vasquez, 1957), southward to the Provincia de Sandia, Departamento de Puno, and west of the Andes from Departamento de Lima, south to Arequipa, Departamento de Arequipa (de la Puente, 1951:35). According to de la Torre (1956), *Mormopterus peruana* J. A. Allen is a synonym of *Tadarida brasiliensis*. The Peruvian subspecies is probably *T. b. brasiliensis* (I. Geoffroy), but the status of *T. brasiliensis* in Perú is open to question.

Tadarida macrotis (Gray)

The only known Peruvian specimens are from near Marcapata, Departamento de Cuzco (Sanborn, 1951*a*).

Tadarida similis Sanborn

This bat has been recorded east of the Andes from near Marcapata, Departamento de Cuzco (Sanborn, 1951*a*), and west of the Andes from the Provincia de Lima, Departamento de Lima (de la Puente, 1951:38).

Mormopterus kalinowskii (Thomas)

Kalinowski's bat is known west of the Andes from Trujillo, Departamento de La Libertad (USNM 283175 and AMNH 165625-165627), and from Chosica, 2800 feet, Departamento de Lima (USNM 103928); from east of the Andes it has been recorded from *Hacienda Limon, near Balsas, Río Marañón, Departamento de Amazonas (Osgood, 1914). The locality given for the holotype was "Central Peru" (Thomas, 1893).

Mormopterus phrudus Handley

Two individuals from the type locality at Machu Picchu, 6000 feet, Departamento de Cuzco, are the only specimens known (Handley, 1956).

Molossus ater É. Geoffroy St.-Hilaire

Black mastiff bats have been recorded from Shapaja and Juan Guerra, Departamento de San Martín (Jamet and Vasquez, 1957), and from Tingo Maria, 2000 feet, Río Huallaga, Departamento de Huánuco, south to near Marcapata, Departamento de Cuzco (Sanborn, 1951*a*). *M. ater* also has been reported (under the name *M. mysurus*) from the "region of Ceja, 5000 feet above sea level on the eastern slopes of the Central Cordillera" (Tschudi, 1844:85). The only Ceja that I have been able to locate in Perú is on the western slope of the Cordillera, about 3000 feet, Departamento de Arequipa. For the use of *M. ater* in place of *M. rufus* see Goodwin (1960).

Molossus molossus (Pallas)

Distribution. Occurs throughout most of Perú from sea level to 9000 feet in Andes (Dobson, 1878:412). Recorded east of Andes from Pebas, Río Amazonas, Departamento de Loreto (Thomas, 1928*c*), south to near Marcapata, Departamento de Cuzco (Sanborn, 1951*a*), and west of Andes from Piura, Departamento de Piura (Miller, 1913), and Eten, Departamento de Lambayeque (USNM 155538-155543).

Remarks. See Husson (1962:256-258) for the correct specific name of this bat. Free-tailed bats were netted among huts at Nevati and appeared to be emerging from palm-thatched roofs. The subspecies reported from west of the Andes is *M. m. daulensis* J. A. Allen (Aellen, 1965). *M. m. crassicaudatus* É. Geoffroy St.-Hilaire has been reported from the Guayanas south to Argentina, and *M. m. major* (Kerr) has been reported from Colombia and Venezuela. Dr. Karl F. Koopman has kindly examined a large number of small *Molossus* represented by specimens from Panamá to Guayana and Argentina, and he tentatively recognized *M. m. daulensis* J. A. Allen from northwestern Perú and *M. m. crassicaudatus* from the Amazon basin of Perú.

Specimens collected (7). Nevati, 7.

Promops davisoni Thomas

This bat is known west of the Andes from Talara, Departamento de Piura, south to Barranco, Chosica (type locality), Matucana, and Miraflores, all in Departamento de Lima (de la Puente, 1951:39-40).

Eumops auripendulus (Shaw)

Temminck's mastiff bat has been recorded west of the Andes from *Mallares Provincia de Sullana, Departamento de Piura (Aellen, 1965), and east of the Andes from Guayabamba (=Santa Rosa de Huayabamba), Departamento de San Martín (J. A. Allen, 1897; Goodwin, 1953:259), Pucallpa, Río Ucayali, Departamento de Loreto (Sanborn, 1949*b*), and from Vista Alegre and Hacienda San Antonio, Río Chinchao, both in Departamento de Huánuco, southward to the Colonia del Pereni [Perene], Departamento de Junín (Sanborn, 1932*b*).

These records include specimens previously reported as *Eumops abrasus* (see Goodwin, 1960). Two subspecies have been reported from Perú, *E. a. auripendulus* (Shaw) to the west of the Andes and *E. a. milleri* (Allen) to the east.

Eumops perotis (Schinz)

The greater mastiff bat is known west of the Andes from the Provincia de Lima, Departamento de Lima (de la Puente, 1951:42), and east of the Andes from Juan Guerra, Río Ponasa [Ponaza], and *Rumispa, both in Departamento de San Martín (Jamet and Vasquez, 1957), and from the Departamento de Loreto (no exact locality—Sanborn, 1932*b*). Sanborn's record from Loreto substantiates the occurrence of *E. p. perotis* (Schinz) east of the Andes, but it is possible that the specimens cited by Jamet and Vasquez represent misidentified *Eumops trumbulli*. The specimens reported by de la Puente (1951) as *E. p. californicus* from the west coast of Perú are instead *E. p. perotis* (see Smith and Genoways, 1969).

Eumops trumbulli (Thomas)

The only Peruvian localities of record for this bat are Yarinacocha, Río Ucayali, and Alto Río Nanay (Sanborn, 1932*b*) both in Departamento de Loreto (Sanborn, 1949*b*). Fifteen specimens reported from *[Puerto] Indiana, Río Amazonas, Departamento de Loreto as *Eumops perotis* (Pirlot, 1968) probably represent additional records of *Eumops trumbulli* according to Smith and Genoways (1969).

SPECIES ERRONEOUSLY REPORTED FROM PERU

Cabrera (1957:67) and more recent authors have listed *Phyllostomus discolor* (Wagner) as occurring in Perú. Apparently, the only Peruvian record is based on *Phyllostoma innominatum* Tschudi (1844:62). Tschudi noted that he had not examined specimens and that he was applying the name *innominatum* (literally meaning unnamed) to a bat described by Pöppig (1832). Pöppig reported that he had found a new kind of *Phyllostoma* that changed the number of teeth with age and showed great variation in coat color. Pöppig's description indicates that his series probably included several different genera. Thus the name *P. innominatum,* designated by Tschudi, is a *nomen dubium,* based on a composite. *P. discolor* probably ranges into eastern Perú, but no valid records are known to me.

If Tschudi (1844:74-75) correctly described a Peruvian bat, listed as *Vespertilio velatus* Fischer, it could not, according to Peters (1875), have been the bat now known as a synonym of *Histiotus velatus* (I. Geoffroy St.-Hilaire). Apparently, there are no valid records of *H. velatus* for Perú.

LIST OF COLLECTING STATIONS, 1963-64

Nevati

Departamento de Pasco, Provincia de Oxapampa, 900 feet, *Nevati, latitude 10° 21′ N, longitude 74° 51′ W.

Dates of collecting. 15-18 June 1963, 2-28 July 1964.

Habitat. Nevati is a mission station surrounded by a village of about 250 Campa Indian inhabitants. It is located on the north bank of the Río Pichis, about 10 km. SE Puerto Bermudez. The surrounding land is undulating and the virgin evergreen forest is 60-120 feet tall. Netting was done among the palm thatched huts of the village, among flowering cashew trees, and in nearby gardens where bananas were grown.

San Pablo

Departamento de Pasco, Provincia de Oxapampa, 900 feet, *San Pablo, latitude 10° 27′ N, longitude 74° 52′ W.

Dates of collecting. 2-22 July 1964.

Habitat. San Pablo is a Campa Indian village of about 175 inhabitants located in undulating country on the east bank of the Río Azupizu. Most netting was done in or near the village. Netting in the virgin evergreen forest was poor except for a single area about a kilometer east of the village where there were large rubber trees. At that place most of the low vegetation had been cleared away by the Indians who harvested rubber. The most successful netting was done in small gardens where bananas, papayas, and other fruits were grown.

San Juan

Departamento de Pasco, Provincia de Oxapampa, 900 feet, *San Juan, latitude 10° 30′ N, longitude 74° 53′ W.

Dates of collecting. 22 July-29 August 1964.

Habitat. San Juan is a Campa Indian village, population about 75, located on the east bank of the Río Azupizu about 5 km. from San Pablo. Immediately behind the village to the southeast is a sharply rising hill that reaches an elevation of about 2000 feet. Beyond, the country becomes rugged, with large hills and many cliffs. San Juan is surrounded by virgin evergreen forest 60-120 feet tall. Most netting was done at the southwest end of the village where the Indians were clearing the forest to extend a landing strip used by mission planes. Bat netting always seemed to improve considerably immediately following additional clearing. Nets set across a shallow stream and in the forest across a 15-foot-wide trail south of the village also were productive. Many bats collected near San Juan were shot from their day roosts within a 6-kilometer radius of the village.

San Ramón

Departamento de Junín, Provincia de Tarma, 2900 feet, 3 km. NW San Ramón, latitude 11° 8′ N, longitude 75° 22′ W.

Dates of collecting. 25-29 June 1964.

Habitat. Netting was done over a stream that varied from 10-20 feet in width, over a trail above the stream in dense secondary growth, and along the lower edge of a plantation between the stream and a small sawmill. Many bats netted over the trail had been attracted to the area by several large fig trees *(Ficus)* with ripe fruit. Nets set along the lower edge of the plantation were near ripe papayas.

Tarma

Departamento de Junín, Provincia de Tarma, 7300-7900 feet, 32-35 km. NE Tarma, latitude 11° 14′ N, longitude 75° 29′ W.

Dates of collecting. 17-24 June 1964.

Habitat. Netting was done near and over a stream 12-15 feet wide at places 600-800 feet from where it joined the Río Palca. Nearly vertical canyon walls extended upwards on both sides of the stream valley for more than 1000 feet. Brushy forest (10-35 feet tall) bordered the stream, giving way to scattered shrubs, grass and rocky cliffs within 150 feet. Most of the *Anoura* were shot in a tunnel used by a large power plant at 7900 feet, 32 km. NE Tarma. All other specimens were netted at 7300 feet, 35 km. NE Tarma.

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THE TURTLES AND CROCODILES OF THAILAND AND ADJACENT WATERS

With a Synoptic Herpetological Bibliography

By

Edward H. Taylor

VOL. XLIX PAGES 87-179 Nov. 12, 1970 No. 3

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The Turtles and Crocodiles of Thailand and Adjacent Waters With a Synoptic Herpetological Bibliography[1]

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ABSTRACT

The entire known turtle and crocodile faunas of Thailand and adjacent waters are treated, based on collections in Chulalongkorn University in Bangkok and in part on specimens in the EHT-HMS collection in Lawrence, Kansas. The number of species and subspecies here reported is 23 turtles and 3 crocodiles. Certain other specimens of turtles in the Bangkok Zoological Gardens purporting to be from Thailand have been examined. Some of these may also have a place in the Thai fauna, but their provenance is uncertain, some certainly not from Thailand.

INTRODUCTION

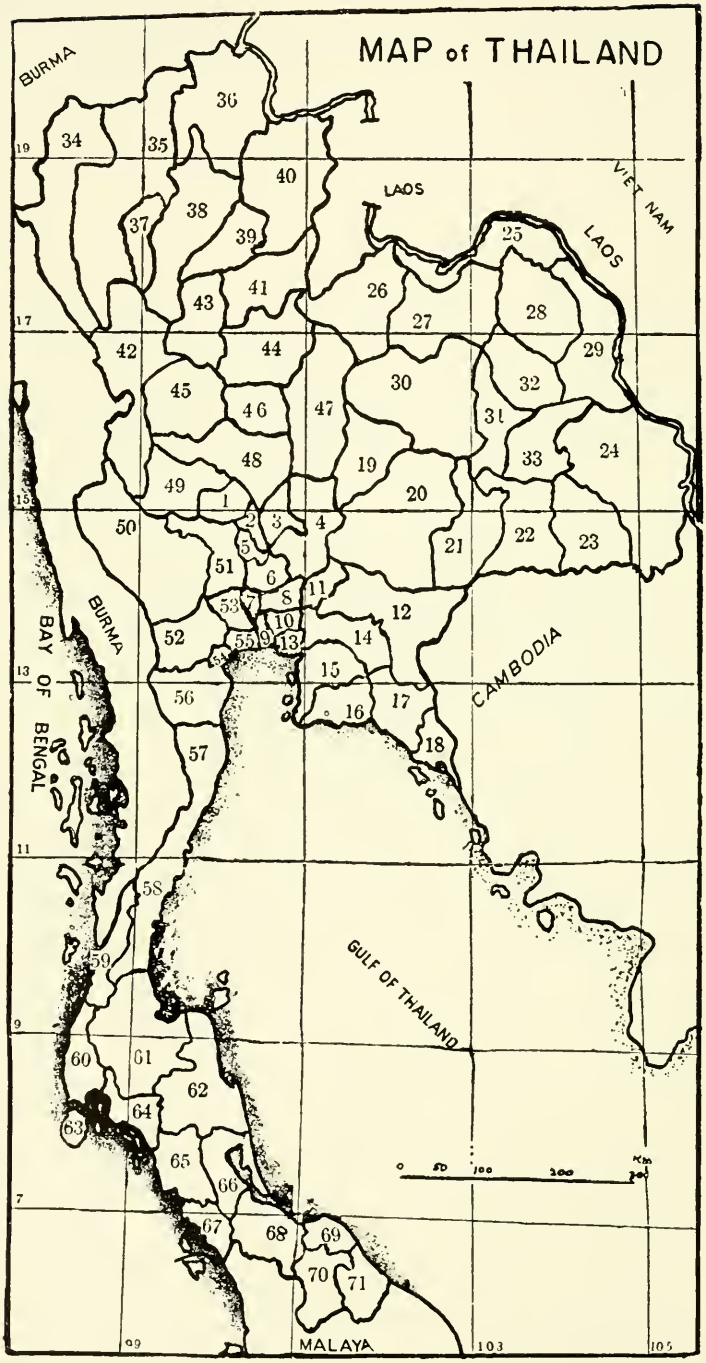
This is the fourth of a series of publications on the herpetological fauna of Thailand. The three others deal with the Amphibia (Taylor, 1962b), Sauria (lizards) (Taylor, 1963b), and Serpentes (Taylor, 1965a). This work treats of the Thai Testudines and Crocodylia, together with a synoptic bibliography for the series.

The collections on which these works were based were made chiefly during my sojourns in Thailand, 1958-59, 1961-62, while holding Fulbright Fellowships. These were made available through the kind help of Dr. Supachai Vanijuvadhana, then Secretary General of Chulalongkorn University of Bangkok, Thailand, who was himself greatly interested in the Thai faunas. I was in residence a total of more than 26 months, and of this time more than half was spent in exploration in various parts of the Kingdom. A third journey of about two months duration was made in 1964. This time was spent in the field.

For the most part the synonymies and literature lists refer to articles dealing with Thai specimens or specimens from localities in closely adjoining territory. Where available, Thai specimens were used for the descriptions. Unless otherwise designated, the numbers are those of specimens (at least formerly) in the collections of Chulalongkorn University.

I have included a map of Thailand showing the Changwats (provinces). The numbers have no significance—merely referring to the names.

[1] This work was done under National Science Foundation Grant No. GB-4510.



MAP 1. Provinces (Changwats) of Thailand. The numbers refer to the adjoining list of provincial names, and have no significance in themselves.

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M. L. Pootipong Nupartpat Varavudhi, an instructor in Chulalongkorn University, accompanied me on many of my earlier journeys of exploration and proved an excellent companion and collector as well as interpreter. I have received much help from Mr. Oliver Gordon Young and his father, Mr. Harold Young, of Chiang Mai, Thailand, both for specimens and for much needed transportation. I am also under very considerable obligation to Dr. Boonsong Lekagul, Secretary General of the Association for Conservation of Wildlife, for his help in collecting, for specimens and for his companionship on numerous collecting trips.

The names of many other persons, whose help has been acknowledged elsewhere in the series, might well have been repeated here.

List of Thai Changwats (Provinces)

Spellings as used by the U.S. Army Gazetteer, 1944.

1. Chainat
2. Sing Buri
3. Lop Buri
4. Sara Buri
5. Ang Thong
6. Ayutthaya
7. Nonthaburi
8. Pathum Thani
9. Thon Buri
10. Phra Nakhon (Bangkok)
11. Nakhon Nayok
12. Prachin Buri
13. Samut Prakan
14. Chachoengsao
15. Chon Buri
16. Rayong
17. Chanthaburi
18. Trat
19. Chaiyaphum
20. Nakhon Ratchasima (Khorat)
21. Buriram
22. Surin
23. Khu Khan (Sisaket)
24. Ubon
25. Nong Khai
26. Loei
27. Udon Thani
28. Sakon Nakhon
29. Nakhon Phanom
30. Khon Kaen
31. Maha Sarakham
32. Kalasin
33. Roi Et
34. Mae Hong Son
35. Chiang Mai
36. Chiang Rai
37. Lamphun
38. Lampang
39. Phrae
40. Nan
41. Uttaradit
42. Tak
43. Sukhothai
44. Phitsanulok
45. Kamphaeng Phet
46. Phichit
47. Phetchabun
48. Nakhon Sawan
49. Uthai Thani
50. Kanchanaburi
51. Suphan Buri
52. Rat Buri
53. Nakhon Pathom
54. Samut Songkhram
55. Samut Sakhon
56. Phet Buri
57. Prachuap Khiri Khan
58. Chumphon
59. Ranong
60. Phangnga
61. Surat Thani
62. Nakhon Si Thammarat
63. Phuket
64. Krabi
65. Trang
66. Phatthalung
67. Satun
68. Songkhla
69. Pattani
70. Yala
71. Narathiwat

TESTUDINES

General Consideration of the Testudines

A considerable number of the herpetologists of the 19th century contributed to the understanding and description of the species, genera, families, and higher groups of the turtles. Cope proposed a suborder Athecae for the huge sea turtle (Leathery Turtle) thus separating the one family, genus, and species (two subspecies) from all other turtles. This has been rather generally accepted by herpetologists. However, Mertens and Wermuth, 1955, in a critical list of the recent turtles, do not recognize the suborder Athecae but place its family Dermochelydidae with the family Cheloniidae under a Sectio Chelonioidea (superfamily?), a treatment which may be questioned.

Boulenger's "Catalogue of the chelonians, rhynchocephalians, and crocodiles" published in 1889 served largely as a guide to turtle classification. In 1909 Siebenrock published his "Synopsis der rezenten Schildkröten mit Berücksichtigung der in historischer Zeit ausgestorben en Arten." This tended to replace as a guide the earlier listing of Boulenger. Williams (1952) offered a tentative arrangement of the Testudinata of the world. The more recent work is that of Mertens and Wermuth (1955), "Die rezenten Schildröten, Krokodile und Brückenechsen: eine kritische Liste der heute lebenden Arten und Rassen."

J. E. Gray, who was largely responsible for the description of genera and species of Asiatic turtles, was able to recognize a number of genera which Boulenger disregarded or rejected. Certain of these were resurrected by Siebenrock (1909). Malcolm A. Smith (1931a), who treated the Eastern Asiatic turtles, also revived certain of Gray's genera. Still others have been resurrected by later authors.

The living turtles now in the zoos in Chiang Mai and Bangkok have for the most part come from various localities in Thailand. However, I am informed that a few have certainly come from neighboring states, and their presence in captivity does not necessarily place them as members of the Thai fauna. I am quite certain, however, that some forms reported in the neighboring parts of Malaya, Burma and in the Indo-China area do occur and and will be added to the Thai list of endemic forms sooner or later.

There is a temple in Bangkok where Thais bring turtles and free them, thus "saving their lives" and by this, gaining merit for a Buddhistic future. I am unaware of the subsequent care of the animals. There are also shops where turtles may be purchased for food in Bangkok and other Thai cities. Thus there is always much traffic in turtles and this offers opportunity for introduction of alien species.

The Testudinate Fauna of Thailand

The species of turtles or tortoises of Thailand are far less numerous than those of the other three herpetological groups (Amphibia, Serpentes, Sauria). The greater number of the species are aquatic (marine or fresh water). Certain ones, however, are completely terrestrial while certain others may be found at least temporarily away from their water habitat. Unlike fishes, most turtles must leave the water or lift the head above water in order to breathe, since they are typically air breathers. Many species occasionally emerge from the water and take a perch on a rock, or log, or they may be seen swimming with their heads above the water surface. Some species are reputed to be capable of limited anal respiration when submerged.

The marine forms are accustomed to return to land to deposit their eggs in pits dug by the female along sandy shores. This pit, one or two feet deep, is prepared by the female shortly after her arrival and then a series of eggs is laid, often as many as 100 or more. These, which may be in several layers, are then covered by pulling in sand to fill the pit above the eggs. Then the female, to conceal the pit location, disturbs the sand for some distance in the neighborhood of the pit so its exact locality is not obvious. The females may lay several times during a season; some species reputedly laying as many as 400 or 500 eggs in a year.

When the young hatch they instinctively burrow to the surface and then move directly toward the water, which they enter, fully equipped for swimming, and breathing, and food finding!

In Thailand it is customary for the government to lease certain areas along the coasts to egg-collectors. The eggs are sought out and dug up to be used as food. They may be consumed locally or they may be marketed at a considerable distance. Seemingly there is always a market for all eggs gathered.

The government also collects a certain number of eggs which are hatched in incubators or sorts, and after a time these young are set free in coastal waters. This presumably is to assure a future breeding population if the egg collectors have been too assiduous. I have observed a release of this type made at the naval station at Sataheep, Thailand.

Locomotion. No known species of turtle has lost its arms or legs. However, the species that entered the ocean have modified the limbs into paddles which externally show little of the original form of these appendages. Occasionally the tip of a digit bearing a claw may be seen, but concealed within the paddle the original large limb bones may be nearly complete, together with at least many of the digital elements.

Oviposition. Malcolm Smith (1931a, pp. 61-62) gives an excellent description of the egg-laying of the Leathery Turtle and subsequent happenings. I quote: "The hole is dug fifteen or twenty meters away from the water's edge

and is much deeper than that made by other Marine Turtles. Like the Green Turtle, the Luth, while digging her nest and depositing the eggs, is completely indifferent to the presence of spectators or noises of any kind. After covering up the eggs, the sand is ploughed up all around for a considerable distance so that, unless the spot has been noted at the time, it is almost impossible afterwards to locate the exact position. May and June are the chief months for oviposition, but eggs are found all the year round. Between 90 and 150 are deposited at a time and several batches are laid during the year. Normally the eggs vary from 50 to 54 mm in diameter but ten or fifteen eggs in each nest are abnormal, being either very small and round or dumbbell-shaped, or of the usual size, but ellipsoid. These eggs are infertile. The period of incubation is 65-70 days. The young as soon as they are born can swim fast and dive easily."

TAXONOMIC TREATMENT

Order TESTUDINES

TESTUDINES Batsch, Versuch einer Anleitung zur Kenntnis und Geschichte der Thiere und Mineralien, vol. 1, 1788, p. 437.

TESTUDINATA Oppel, Die Ordnungen, Familien und Gattungen der Reptiles. . . . München, 1811, p. 3.

"A group of animals with the major part of their skeletons on the outside of their bodies."

Body above with a bony carapace, and below with a bony plastron covered with scutes or scales or, in certain forms, by a leathery covering external to the bones. Ribs attached between two vertebrae have only a single head. Bony dermal materials usually close areas between ribs and likewise cover the vertebrae. Girdles supporting limbs are internal to the ribs. Scapula and coracoid separate; clavicles and interclavicle fused to plastral elements; no sternum present; pelvic girdle free, not incorporated in plastral elements.

Teeth never present; jaw edges covered with a heavy keratin sheath. Limbs pentadactyl, digits free, webbed, or incorporated in paddlelike structures. Male copulatory organ single.

The ancient history of this strange group of animals—strange despite the fact that they are known to most people—is practically unknown, owing to the fact that this chapter of earth history has so far been carefully concealed from the searching eyes of the paleontologist. In the Triassic fossil turtles of various sorts are found that do not differ too greatly from those now living. One may postulate that they existed in the preceding Permian and not impossibly in still earlier periods. However, no adequate proof has been presented of their evolution from other specific reptilian groups that preceded them.

The habits of these animals are very diverse. A few are fitted for a terrestrial existence, but the bulk of the genera and species have been driven

to an aquatic existence presumably because they were better equipped to compete with aquatic animals for food than with their terrestrial competitors.

The purely terrestrial genera are few: *Testudo, Gopherus, etc.* For the most part these manage to exist in areas either isolated from large populations of man or in areas undesirable to competitors. They are, perhaps for the most part, vegetarians, or omnivorous, and are able to maintain their populations by the production of large numbers of eggs, by their ability to withstand hunger for considerable periods of time, and in having a very long life-expectancy.

Despite the diversity of habitat, oviparity is the only method of reproduction, and it is necessary for these aquatic animals to revert to the land for finding suitable places to deposit their eggs. Marine forms utilize the sea beaches, preferably in sandy areas, while fresh water species lay eggs in river banks or shoals. Some river forms even go to higher areas near rivers, or land high enough to escape overflow, and even to the top of nearby hills.

Sea turtles seemingly find it easy to excavate pits to deposit their eggs but turtles that must dig in hardened earth find it necessary to moisten hard dry earth with their urine to soften the surface and if this does not suffice they may return to the water source to fill up their accessory bladders with water and carry this again to the egg-laying area in order to help complete the excavation.

Many turtles have rather an elaborate courtship pattern. One general pattern may obtain in several genera, or perhaps even throughout an entire family. In some species this pattern of behavior may be repeated for several days before actual copulation occurs.

Turtles are a source of human food and both turtles and their eggs are preyed upon by man. In areas where they were once numerous a species may become completely extinct by the advent of man in numbers.

Suborder Athecae Cope

ATHECAE Cope, Amer. Assoc. Adv. Sci., vol. 19, 1870, p. 235; Boulenger, Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Mus., 1889, p. 7; Fauna of British India. . . 1890, p. 50; Hay, Proc. U.S. Nat. Mus., vol. 73, (3), 1928, p. 6.
CHELONOIIDEA (part.) Siebenrock, Zool. Jahrb., Jena, Suppl. 10, 1909, p. 544.
CHELONIOIDEA Mertens and Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 386 ("Sectio").

Only a single family recognized.

Family **Dermochelydidae** Siebenrock

Sphargidae Gray, Ann. Philos., vol. 10, 1825, p. 212.
Dermochelyidae Siebenrock, Zool. Jahrb., Jena, Suppl., Band, 10, 1909, p. 551.

The family has only a single genus, *Dermochelys*. It occurs in the Atlantic, Pacific, and Indian Oceans, and in the Mediterranean Sea.

Genus **Dermochelys** Blainville

Dermochelys Blainville, Bull. Soc. Phil., 1816, p. 119. (Type of genus, *Testudo coriacea.*)
Sphargis Merrem, Syst. Amphib., 1820, p. 19.
Coriuda Fleming (type, *coriacea*), Phil. Zool., 2, 1822, p. 271.
Seytina Wagler (type, *coriacea*), Isis von Oken, 1828, p. 861. (Substitute name for *Sphargis.*)
Dermatochelys Wagler, Natürliches System der Amphibien mit vorangehender Classification der Saügethiere und Vögel, 1830, p. 133 (type, *coriacea*).
Chelyra Rafinesque (type, *coriacea*), Atlantic Jour., vol. 1, 1832, p. 64.

Diagnosis: Large sea turtles, the young covered with small polygonal shields, largest ones on the soft leathery carapace and plastron. Adult with smooth skin. Young with 7 dorsal keels on carapace and 5 on plastron, the keels covered by raised quadrangular scutes. More or less symmetrical plates or scutes on head, the occipital usually the largest. Tail very short. Arms large flattened paddles; legs, shorter flattened paddles. Only a single living species known.

Dermochelys coriacea (Linnaeus)

Testudo coriacea Linnaeus, Systema Naturae, ed. 12, 1766, p. 350 (type-locality [restricted], Palermo, Sicily).
Dermatochelys coriacea, Günther, Reptiles of British India, 1864, p. 55.
Dermochelys coriacea, Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History), 1889, p. 10; Fauna of British India . . . Reptilia and Batrachia, 1890, p. 50; Siebenrock, Zool. Jahrb., Jena, Suppl., vol. 10, 1909, p. 553; Deraniyagala, Proc. Zool. Soc. London, 1930, pt. 3, pp. 1057-1070; Ceylon Jour. Sci., Sec. B, vol. 16, 1930, p. 45; Ceylon Jour. Sci. Colombo Museum Nat. Hist. Ser., vol. 1, 1939, pp. 38-102, figs. 12-34; M. Smith, The Fauna of British India including Ceylon and Burma, Reptilia and Amphibia, vol I, Loricata, Testudines, 1931, pp. 59-62, figs. 6-8.
Sphargis coriacea, Tickell, Jour. Asiat. Soc. Bengal, vol. 31, 1863, p. 367-370. 1 colored plate.
Dermochelys schlegeli, Stejneger, Bull. U.S. Nat. Mus., No. 58, 1907, p. 485.
Dermochelys coriacea schlegeli, Garman, Bull. U.S. Nat. Mus., 1884, No. 25, p. 303 (type-locality, Guaymas, Sonora, México); Carr, Handbook of the turtles of the United States and Canada, 1952, p. 452; Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, 1955, p. 387; Lekagul, Conserv. News, Bangkok, No. 7, 1965 (1966), p. 19, fig.

Diagnosis: Characters of the family and genus.

Atlantic forms differ from those in the Pacific and Indian Oceans so that two subspecies are recognized, only one of which occurs in Thailand waters.

Dermochelys coriacea schlegeli (Garman)

Sphargis coriacea var. *schlegeli* Garman, Bull. U.S. Nat. Mus., No. 25, 1884, p. 303 (type-locality [restricted], Guaymas, Sonora, México). (The type is figured in Temminck and Schlegel.)
Sphargis angusta Philippi, An. Univ. Santiago de Chili, vol. 104, 1899, p. 728 (type-locality, Tocopila, Chile).
Dermochelys coriacea schlegeli, Carr, Handbook of the Turtles of the United States and Canada, 1952, p. 452; Mertens and Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 387.
Dermochelys coriacea M. Smith, The fauna of British India including Ceylon and Burma, Reptilia and Amphibia, vol. 1, Loricata, Testudines, 1931, pp. 59-62 *(part.).*

The status of *schlegeli* as a subspecies is based largely on the fact that the average known size of the Pacific form of *coriacea* is larger than that in the

Atlantic. There are other small differences recorded but it is not certain that these are constant. No one has been able to make a direct comparison of a series of these huge animals. Carr *(loc. cit.)* reports specimens with a body two meters in length—in fact, one reported from Australia reached nine feet in length. Other specimens are reported as weighing from 800 to 1600 lbs.

Compared with the typical form the head is said to be proportionally longer, the scales of the head less symmetrical, and the arms shorter in proportion to length.

Description: In young animals, body and limbs covered with small, irregular, usually polygonal shields. These larger on carapace and plastron than on other parts. Seven keels on dorsal part of carapace, made of larger raised quadrangular shields; five keels on plastron, the median often presenting a double row. These keels may converge and meet anteriorly and the three median meet posteriorly. Scutes on remainder of surfaces smaller, nearly uniform except for a few larger series on edges of limbs.

These shields or scales tend to disappear completely in older animals, but traces of the keels remain visible on carapace as nodular ridges. Keels on plastron tend to disappear completely. Arm bones encased in long fleshy paddles which, in the young, approach length of carapace, but become proportionally shorter in adult.

Color: The adult is colored—"Dorsally a slaty black with three or four longitudinal rows of small white spots not larger than the iris extending between each pair of carapace ridges. These spots are more numerous at the base of the flippers. Head black with a few white blotches. Jaws white, clouded with black. Neck with five longitudinal rows of white spots. Ventrally pinkish white or white, usually with dark reticulation representing scale marks. A black lateral band usually extends from the inguinal area to the cloaca. Sometimes in females the black disappears more or less from the plastron. The top of the caudal crest is white. Newly hatched young are an intense blue black marked with white to whitish; the encroaching black imparts a bluish appearance." Deraniyagala (1930a).

The markings on the adults are similar to those of the young but probably less well defined.

Measurements: Total length, 7 ft. 5 in.; length of carapace, 5 ft. 3 in.; carapace width, 2 ft. 10.5 in.; width of flipper to flipper, 4 ft. 3 in. (From Carr, 1952.)

Remarks: One Thai specimen is figured by Dr. Boonsong Lekagul (1966).

Superfamily **Cryptodira**

Shell with plastron and carapace fused laterally and covered with epidermal horny plates or scales. Head can be withdrawn within shell, the neck

forming a sigmoid bend in a vertical plane. Pelvic girdle not fused to carapace or plastron; pterygoid bones form a median suture for greater part of their length, usually narrowed in their middle. Area above tympanic cavity notched, not roofed over; squamosals and parietals widely separated; fingers and toes distinct, usually with three or less phalanges; four or five claws present. A set of marginals connecting with ribs.

The greater number of Asiatic turtles are associated in this superfamily which includes the families *Platysternidae, Emydidae,* and *Testudinidae.*

Family **Platysternidae** Gray

Platysternidae Gray, Supplement to the catalogue of shield reptiles in the collection of the British Museum, pt. 1, Testudinata (tortoises), 1870, p. 69.

This family was based on a single genus and species—*Platysternon megacephalum* Gray, confined to southeast Asia. This arrangement has been accepted by almost all subsequent students of the Testudines.

Head large, the neck retractile within shell; jugal completely surrounded by bones not forming part of orbital border; temporal region completely roofed over with bones; phalanges with condyles; five claws on hand, four on foot; nuchal bone lacking a riblike process; plastron separated from carapace by several intercalated inframarginals. Tail greatly elongated, covered above and below with heavy scutes, the median dorsal ones keeled; at base of tail and on thighs numerous enlarged conical scales.

Genus **Platysternon** Gray

Platysternon Gray, Proc. Zool. Soc. London, 1831, p. 106 (type of genus, *megacephalum*).

Diagnosis: Plastron much smaller than opening of carapace, connected with carapace by ligamentous tissue. Head large, with powerful jaws covered with a horny shield, the back part of which shows what appear to be lines of growth; upper jaw strongly hooked, extending beyond mouth; five fingers with claws; four toes with claws, the webbing not quite reaching base of claws; scutes on tail quadrangular, arranged in transverse as well as longitudinal lines; axillary and inguinal scent-glands.

Some Thailand specimens of this turtle seem to vary considerably. Thus a young specimen figured and described by Taylor and Elbel (1958) shows considerable difference in shape from the adult type of carapace. There are five costals, the vertebrals being considerably wider than the costals. The lateroposterior marginals are larger than the three posterior costals. The posterior margin of shell is serrated.

This specimen, which had lost its tag, was said to be "practically certain that it came from Dan Sai district in the province of Loei." Certain other older specimens from Phu Kading mountain, 5000 ft., Loei Province, do not show these characteristics.

Platysternon megacephalum Gray

Platysternon megacephalum Gray, Proc. Zool. Soc. London, 1831, pp. 106-107; Illustration of Indian Zoology, vol. 2, 1834, p. 62 (type-locality, "South Chine"); Stejneger, Proc. U.S. Nat. Mus., vol. 66, 1925, p. 102; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1927, p. 400-401, fig 1.

Platysternum megacephalum Theobald, Jour. Linnaean Soc., Zool., vol. 10, no. 41, 1868, pp. 17-18; Boulenger, Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum, 1889, p. 46 *(part.)*; Ann. Mag. Nat. Hist., ser. 5, vol. 19, 1887, p. 461, pls. 16, 17; The Fauna of British India including Ceylon and Burma, Reptilia and Batrachia, 1890, p. 44, figs. 13, 14; Siebenrock, Zool. Jahrb., Jena, Suppl. 10, 1909, p. 450; Mell, Arch. Naturg., vol. 7, 1922, pp. 390-475; *ibid.*, Heft 10, 1922, p. 108; M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 1, pt. 3, 1915, p. 155 (Sai Yoke) *(part.)*; *ibid.*, vol. 2, no. 1, 1916, p. 51 ("Western and ? Northern Siam"); The Fauna of British India, including Ceylon and Burma, Reptilia and Amphibia, vol. 1, Loricata, Testudines, 1931, pp. 74-75, fig. 13 (skull) *(part.)*; Pope, The Reptiles of China, Nat. Hist. Cent. Asia, vol. 10, 1935, 1-604; Wermuth, Aquar.—Terrk., Leipzig, Band 5, pp. 161-165; *part.*; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1079-1081, fig. 15.

Two subspecies, *Platysternon megacephalum megacephalum* and *P. m. peguense* are recognized. The first is known only in southern China.

Platysternon megacephalum peguense Gray

(Fig. 1)

Platysternon peguense Gray, Supplement to the catalogue of the shield reptiles in the collection of the British Museum, part 1, 1870, p. 70 (Type-locality, Pegu, Tenasserim, Burma).

Platysternon megacephalum peguense, Wermuth, Zoologische Beiträge Neue Folge, Band 5, Heft 2/3, 1960, pp. 481-482.

Platysternon megacephalum, Mertens and Wermuth, Zool. Jahrb., Syst., Jena, 1955, Band 83, p. 341, *(part.)*; Taylor and Elbel, Univ. Kansas Sci. Bull., vol. 38, pt. 2, Mar. 20, 1958, pp. 1079-1081, fig. 15.

Platysternum megacephalum, Legakul, Conservation News, Bangkok, No. 7, 1966, pp. 56-57, figs.

Diagnosis: Characters of family and genus. Plastron of young and half-grown with a clearly defined longitudinal symmetrical dark marking completely or partially split by a light median line, and with lateral dark projections on each side. A median dorsal keel, dark colored, with one or two lighter spots, and a series of three small black bosses on the two costal series. Markings less conspicuous or absent in old specimens.

Description of subspecies (from No. 1650 Loei Province, Thailand): Carapace much depressed, length much greater, than width, with a median keel present, evident on first and last three shields; costals with slightly elevated points at middle of areolae; nuchal single, 2.5 times wider than long; first vertebral strongly convex anteriorly, much wider than long, notched posteriorly. Measurements in mm of vertebrals and costals, length x width: first vertebral, 28 x 44; second, 31.5 x 43; third, 29 x 44; fourth, 30 x 41; fifth, 39.5 x 37. First costal, 34 x 32; second, 37 x 47; third, 33 x 42; fourth, 34 x 30. On each side 12 marginal scales other than nuchal; supracaudals scarcely notched at their mutual suture, both tectiform; a slight posterior

projection from fifth vertebral wedged between front part of their mutual suture, and a slight emargination on posterior edge of each; some posterior marginals slightly recurved.

Plastron much narrower than opening of carapace; anterior plastral lobe nearly square; front of carapace truncate, posterior end broadly angulate; abdominal shields somewhat concave. A short bridge, its length (30 mm) much longer than posterior lobe. Measurements in mm of median sutures of plastral shields: gulars, 7; humerals, 20; pectorals, 25; abdominals, 12; femoral, 25; anal, 26. A small median azygos scale between gulars and humerals, its length 9 mm; its width, 9.5 mm. Tail longer than carapace; base of tail and dorsal area on back of thighs with numerous large conical scales, some reaching a height of 9.5 mm; about 28 paired quadrangular subcaudals (the 2 or 3 terminal ones may be single) covering ventral surface, and bending up on sides of tail; a median dorsal row of scales, more or less keeled; a lateral row on each side extending to near tip of tail, with occasional ones fused to adjoining scute; a short intercalated row of 4 scales near base; a series of small irregular scutes between plastron and carapace but no distinctive axillary or inguinal scutes present.

Front of arm with large irregular scutes, somewhat wider than long; scutes on posterior face of arm, larger and fewer; leg and thigh with numerous small scutes, those on under posterior face, largest.

Color: Nearly uniform light brown; head same color; underside of marginals and plastron uniform yellowish or yellow-brown.

Measurements in mm of Nos. 1650 and 1651 respectively: Length of carapace, 167, 167; width of carapace, 132, 128; depth of carapace, 51, 53; length of plastron, 132, 136; width of plastron at bridge, 98.5, 99; width of anterior lobe, 63, 68; width of posterior lobe, 71, 74; length of posterior lobe, 56, 62; tail, 198, (broken); width of head, 52, 54.

Variation: An azygos median scale occurs on the plastron of certain specimens from northern Thailand. Another specimen of unknown provenance shows no trace of the azygos scale but the measurements closely approximate those of the described specimen; the nuchal is abnormally divided. This specimen, despite having almost the same measurements, has the carapace glassy smooth with no suggestion left of the sculpturing produced by lines of growth which are strongly pronounced in the described specimen. The latter is anomalous in having a small intercalated scale between the fourth costal and the fifth vertebral (see comment on a young specimen under "Remarks").

Distribution: In Thailand the species has been taken in the provinces of Loei (Dan Sai and Phu Kading), Kanchanaburi (Sai Yoke), and Chiang Mai.

Remarks: Mr. Harold Young, who has the zoo in Chiang Mai, tells me

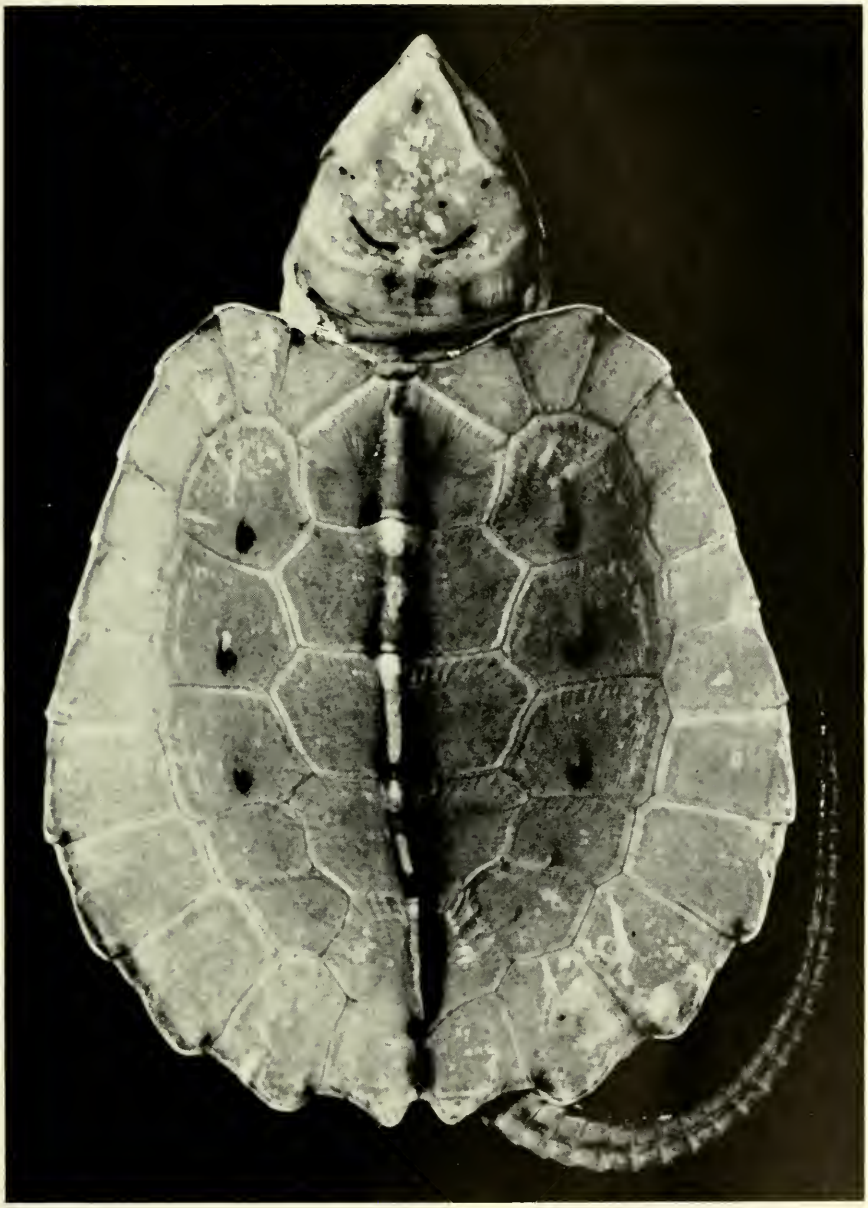

Figure 1. *Platysternon megacephalum peguense* Gray. Kansas U. Mus. Nat. Hist. No. 40084. Lomlo Mt., Thailand. Carapace length, 50 mm; carapace width, 44 mm; tail length, 52 mm.

that this species is very adept at climbing and that the specimens often escape by climbing from the high wire enclosures where they are kept.

The species is usually taken at a considerable elevation along mountain streams. They are reputed to be able to climb trees and shrubs along the streams.

Theobald (1868) reports a specimen from Martaban, Burma. The specimen is very young (shell, 2 in.; tail, 2.25 in.); "color fleshy gray, each of the costal shields with a central black tubercle; beneath bright reddish-orange with a little black above the sutures. Head dark-mottled, with a black-edged yellow stripe behind the eye. Iris pale yellow."

"This species is rare in Pegu, and seems confined to the streams in the hills east of Tonghu, falling into the Sittang and Salwin."

Family **Emydidae** Gray

Emydidae Gray, Annals of Philos., 1825, (2) vol. 10, p. 210.

Head capable of being withdrawn wholly within the shell. Head covered with smooth skin; posterior part of latter usually divided into small scale-like sections. Temporal region not roofed over. Nuchal plate lacking a riblike process; nine bones in the plastron. A bony temporal arch present or absent (may become lost during lifetime of an individual). Median digits with three phalanges; metacarpals elongate; 4 or 5 claws present. Bones of carapace and plastron covered with horny epidermal shields or scutes, those on plastron directly in contact with marginals.

The family has a cosmopolitan range with some 20 genera, 9 of which are represented in Thailand. These are *Cyclemys, Pyxidea, Cuora, Heosemys, Malayemys, Hieremys, Notochelys, Siebenrockiella* and *Batagur.*

Recently McDowell (1964) has proposed two subfamilies; Batagurinae and Emydinae, the former confined to Asia, largely including all the genera listed for Thailand.

Subfamily **Batagurinae**

Batagurinae McDowell, Proc Zool. Soc. London, vol. 143, pt. 2, 1964, pp. 239-279.

Genus **Cyclemys** Bell

Cyclemys Bell, Proc. Zool. Soc. London, 1834, p. 17 (type of genus *C. orbiculata*); Mertens and Wermuth, Zool. Jahrb. Syst., Band 83, Heft 5, 1955 p. 348.

Diagnosis: Shell longer than wide, strongly serrate on posterior border of carapace, less so anteriorly; carapace with 1 or three keels more or less strongly developed. Front lobe of plastron develops a hinge as animal grows older, this between hypoplastral and hyoplastral bones, and only front lobe moves but does not close entirely. Entoplastron intersected by suture. Skull usually with a bony temporal arch. Digits between one-half and completely

webbed. Tail proportionately shorter in adults than in young. Neural plates usually hexagonal in shape, the posterior boundary shortest.

The genus is oriental in its distribution, specimens being known from Burma to Viet Nam, Malaya, Indonesia and Philippines.

Cyclemys dentata (Gray)

(Figs. 2-3)

Emys dhor (part.) Gray, Synopsis Reptilium, pt. 1, 1831, p. 20 (corrected to *dentata* in errata); Illustrations of Indian Zoology, 1830-1835, vol. 2, 1834, pl. 58, fig. 2 (only); (type-locality, Java).

Cyclemys dentata Gray, Catalogue of the shield reptiles in the collection of the British Museum, pt. 1, Testudinata (tortoises), 1855, p. 42, pl. 19; M. Smith, The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia, vol. 1, Loricata, Testudines, Mar. 31, 1931, pp. 80-82, fig. 15; Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, Oct. 31, 1955, p. 348 (synonymy).

Cyclemys dhor, Gray, Supplement to the catalogue of shield reptiles in the collection of the British Museum, pt. 1, Testudinata (tortoises) I, 1870, p. 23; Morice, Coup d'oeil faune Cochinchine, 1875, p. 63; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 131; The fauna of British India, Ceylon and Burma. Reptilia and Batrachia. 1890, p. 30; Siebenrock, Sitzungsb. Akad. Wiss, Wien., vol. 112, Abt. 1, 1903, p. 341; M. Smith and Kloss, Jour. Nat. Hist. Soc. Siam, vol. 1, pt. 4, Dec. 1915, p. 238 (Koh Chang, and "Hup Bon, east of Sriracha"); M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, June 1916, p. 51 ("widely distributed in Thailand; common in certain localities"); M. Smith, Bull. Raffles Mus., no. 3, 1930, p. 8.

Cyclemys orbiculata Bell, Proc. Zool. Soc. London, 1834, p. 17; Monograph of the tortoises having a movable sternum. . . . Zool. Jour. London, 1842, pt. 8, pls. 2-3 (type-locality, India); Theobald, Catalogue of reptiles in the museum of the Asiatic Society, 1868, p. 10; Jour. Linnaean Soc., Zoology, vol. 10, no. 41, pp. 12-13.

Cyclemys oldhami Gray, Proc. Zool. Soc., London, 1863, p. 178 (type-locality, Mergui); Günther, The reptiles of British India, 1864, p. 15, pl. 5.

Cyclemys orala Gray, Proc. Zool. Soc. London, 1863, p. 178 (type-locality, Sarawak).

Cyclemys belli Gray, Proc. Zool. Soc. London, 1863, p. 179 (type-locality, Madras or Bombay).

Cyclemys dhor shanensis Annandale, Rec. Ind. Mus., vol. 14, 1918, p. 67, pl. 20 (type-locality, Inle Lake, Burma).

Diagnosis: A single median keel on carapace, distinct except in aged specimens where only posterior part is indicated; young flattened, adults arched and slightly flattened on dorsum; skin on top of head not divided, except large scute behind eye, which is partly divided, and some small scutes bordering nuchal region; nuchal scute nearly twice as long as wide; longest plastral suture between pectoral scutes; gulars openly emarginate; anal notched; posterior border of carapace serrate.

Description of species (from no. 1641, Bhetong, Yala): Carapace well arched, median dorsal vertebral area somewhat flattened; a distinct median keel, obtuse anteriorly, sharp posteriorly; nuchal (12 x 6.4 mm) much longer than wide; first vertebral scale (28 wide x 25 mm long) wider anteriorly than posteriorly, lateral sutures sinuous; second, third and fourth vertebrals wider than long, wider anteriorly than posteriorly; fifth narrowed anteriorly, widened posteriorly, much wider than long (44 x 25 mm); costals wider than long, first 3 larger than vertebrals, fourth (21 x 24 mm) smaller than

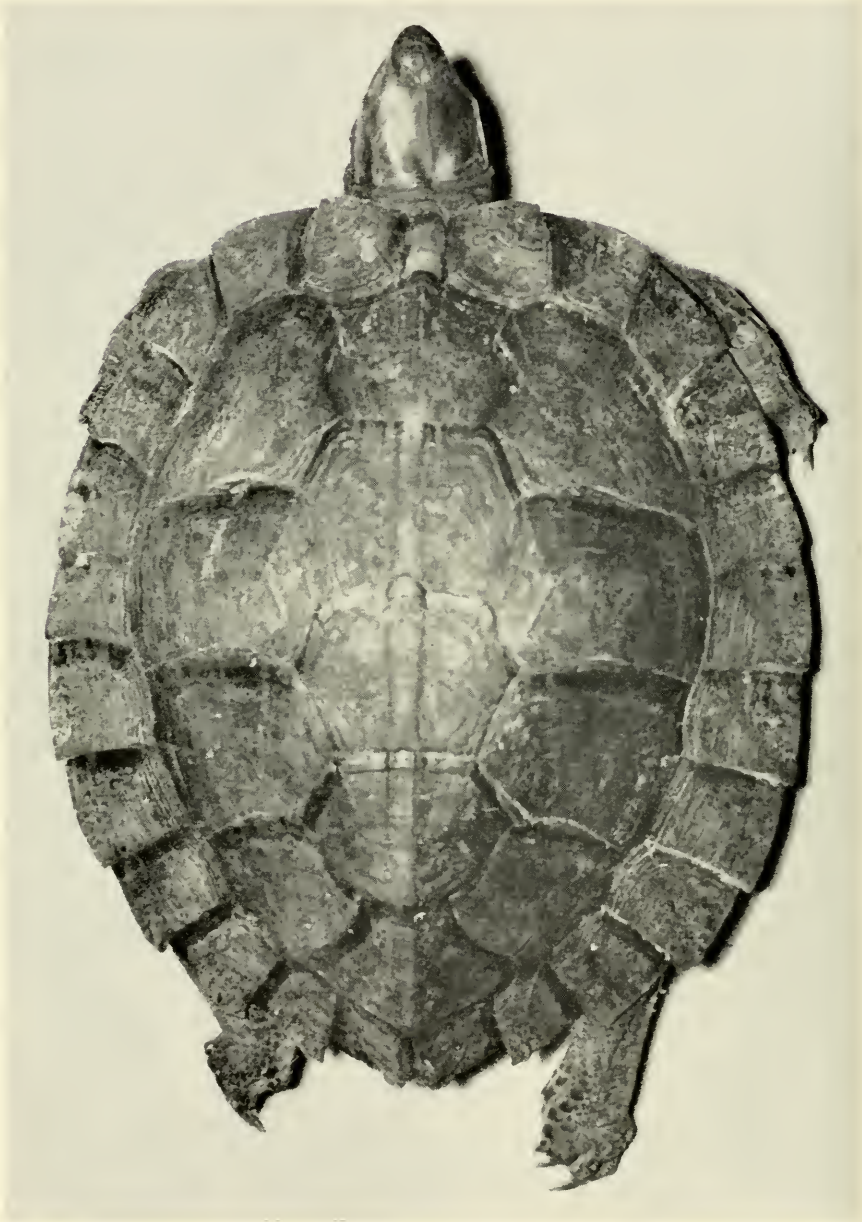

FIGURE 2. *Cyclemys dentata* Gray. Chulalongkorn Univ. No. 1641, Bhetong, Yala, Thailand. Carapace length, 141 mm; carapace width, 124 mm.

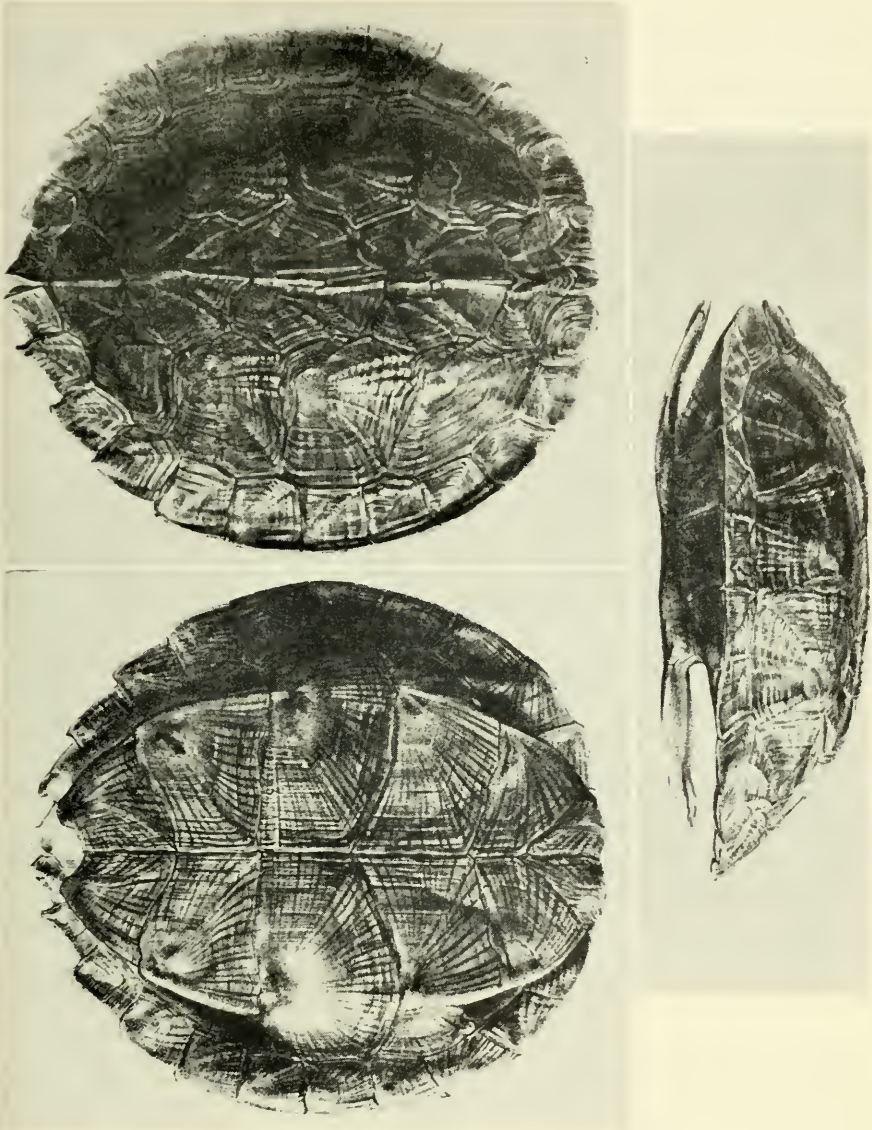

Figure 3. *Cyclemys dentata* Gray. From Gray, Catalogue of the shield Reptiles etc., 1855, pl. xix.

vertebrals; marginal scutes 12 on each side, supracaudal divided, with a distinct notch 3 mm deep; plastron slightly shorter than carapace (12 mm); sutures of plastral scales in following descending order of length: pectorals, abdominals, gulars, anals, femorals, humerals; axillary and inguinal scutes distinct; bridge moderate, approximately 30% of length of plastron.

Head rather small; snout shorter than orbit, projecting but slightly, tip feebly bicuspid; skin on top of head undivided except posterior part; 2 scales lying behind eye; a single scute covering front of upper jaw; lower jaw with a single scute followed posteriorly by an enlarged scute; about 14 rows of small scales precede ear, which is covered with small scales; hands and feet webbed to the claws; front face of arm with about 20 enlarged transverse scales; on posterior face a small patch of 6 or 7 enlarged scales; tail short; foot with about 10 enlarged scales on heel; adjoining them above along edge, another small group of larger scales; tail with paired, somewhat enlarged subcaudals (terminal part of tail missing).

Color: Carapace dark brown to olive-black, nearly uniform, without evidence of black rays; on plastron radiating lines of black and dull yellow, conspicuous from pectorals to anals; gulars and humerals nearly uniform black; head olive-brown above and on sides with black and olive radiating lines on upper and lower jaws; sides of neck yellowish olive with longitudinal black stripes, upper sloping above ear, the next reaching angle of jaws; 7 or 8 stripes separated by dotted lighter lines on throat. Axillary and inguinal regions yellow with a few black dots or marks.

Measurements in mm: Length of carapace, 141; width of carapace, 124; length of plastron, 134; width at posterior end of bridge, 70; width at anterior end of bridge, 58; depth of shell, 55; length of median plastral sutures: gulars, 21; humerals, 14; pectorals, 26.5; abdominals, 23; femorals, 18; anal, 21; width of head, 20; length of head, 24.

Variation: Differences between young and adults are considerable. Malcolm Smith (1931a) states that old specimens may lose the keel entirely, and the serration of the carapace edge is less marked; the vertebrals are broader anteriorly than posteriorly in young and half-grown, while the reverse is true in old specimens. There may be differences in the length of the plastral sutures on the medial line, but usually the pectoral suture is longest. A transverse hinge may develop. The tail is proportionally longer in the young than in the adult. A specimen from Burma is light brown with black spots. The shell may reach a length of 240 mm, 175 mm width, 82 mm depth.

Distribution: In Thailand the species occurs rather widely. Specimens have been taken at the Sanoi River Forestry Station, near the Cambodian border in eastern Ubon; specimens have been reported from "Kampong

Jalor" in Pattani; Hup Bon, and Sriracha in Chon Buri; Ban Kok Klap, in Chumphon. The described specimen is from Bhetong, Yala.

Outside of Thailand the species is known in India, Burma, Cambodia, Malaya, and the Indo-Australian Archipelago.

Remarks: The specimen taken on the Cambodian border of eastern Ubon, although a little larger than the described specimen (141 mm carapace length), has fewer lines of growth and the areolae are much more distinct and rugose. The color is light brown above, the plastron blackish brown with the yellowish radiating lines apparent, especially near the sutures. A yellow line present on the lower jaw. The head above is grayish with fine black flecks; darker and lighter longitudinal lines appear on the nuchal region while the lateral stripes on sides of neck are much less distinct.

Theobald (1868) points out that Bell has stated that this species *(orbicularis)* affords a link between the box tortoises and the more typical Emydidae. However, the describer (Bell) failed to notice the pseudo-hinge, the homologue of the ligamentous hinge in *Cuora* although in *orbicularis* the motion of the two portions is limited, owing to its being the result merely of the permanent non-union of the toothed suture of the pectoral and abdominal bony plates, and not of a special ligamentous division. It is imperceptible in the very young animal, but the motion of the plates develops it as the animal grows and in adult or aged ones is often marked externally by a "carious fossa." This character is evident in the type *oldhami* which Theobald himself collected.

The specimen described by me shows at this stage (total length 143 mm [53.8 in.]), no trace of the hinge or any movement. This was the case of Theobald's 5-inch halfgrown specimen but he mentions "Sternal suture distinct." The color of the plastron "Sternum deep brown or blackish; yellow-rayed," is duplicated in my described specimen.

Genus **Pyxidea** Gray

Pyxidea mouhoti Gray

Cyclemys mouhoti Gray, Ann. Mag. Nat. Hist., ser. 3, vol. 10, 1862, p. 157 (type-locality, "Laos Mountains, Annam-Siam Border"; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History), 1889, p. 132; Fauna of British India. . . . 1890, p. 31; M. Smith, The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia, vol. 1, Loricata, Testudines, 1931, pp. 78-80, fig. 14 (shell); Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, 1955, p. 348.

Pyxidea mouhotii, Günther, Reptiles of British India, 1864, p. 16, pl. 4; Jerdon, Proc. Asiat. Soc. Bengal, 1870, p. 68; Siebenrock, Sitzb. Akad. Wiss. Wien, Band 112, Abt. 1, 1903, p. 345, pl. 1, figs. 3, 4; Schmidt, Bull. Amer. Mus. Nat. Hist., vol. 54, 1937, p. 407.

Diagnosis: Carapace serrate especially posteriorly, and strongly tricarinate. Dorsal part flattened along mesial region. Head lacking stripes. Digits half-webbed.

Description of species: Carapace a little longer than wide, slightly serrate anteriorly, distinctly so posteriorly. Twelve pairs of marginals including supracaudals which are smallest of all. Nuchal scale single, small, narrow. Five vertebral shields usually hexagonal, narrower posteriorly than anteriorly (except first), and wider than long (except last). Four costals on each side (rarely more, 6-7) likewise wider than long. Three keels, median best defined, the 2 lateral keels on costals curving. Plastron smaller than ventral opening of carapace, truncate anteriorly, with notch posteriorly. Plastron attached at a short but distinct bridge, its width equal to one third length of plastron, area of attachment chiefly by hypoplastral bone.

Head medium in size, truncate: snout shorter than orbit. Numerous shields of moderate size on posterior part of head. Front of arm with large imbricating horny shields; legs generally club-shaped, their lower parts covered with imbricate scales pointed at their tip; digits about half webbed. Tail of moderate length, the skin at its base and adjoining areas on thighs with pointed tubercles.

Color: Generally uniform light brown above on carapace; yellowish brown on plastron, with dark areas on each shield. Head brown with dark flecks or small spots; light spots on sides of head.

Measurements in mm: Total length of carapace, 160; width, 112; height, 58. (Description from literature.)

Remarks: The exact type-locality is not known. Mouhot collected along the Thai border and is known to have collected in parts of Eastern Thailand.

Genus Cuora Gray

Cuora Gray, Catalogue of the shield reptiles in the collection of the British Museum pt. 1, Testudinata (Tortoises); 1855, p. 41. Type of genus, *C. amboinensis.*

Cyclemys Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 128; Fauna of British India, Ceylon and Burma. Reptilia and Batrachia. 1890, p. 28 (part); Mertens und Wermuth, Zool. Jahrb., (Syst.), Band 83, Heft 5, 1955, p. 347.

Diagnosis: Plastron hinged, the anterior and posterior parts movable and capable of completely closing opening of carapace, fore and aft. Plastron joined to carapace by ligamentous tissue, not forming a typical bridge. Entoplastron with suture. Skull usually with bony temporal arch (incomplete in a Chinese species). Alveolar jaw surface narrow; digits completely webbed; tail rather short. Only one of the four species is known to occur in Thailand. This is the widespread type-species, *Cuora amboinensis.*

Cuora amboinensis (Daudin)

Testudo amboinensis Daudin, Histoire naturelle, générale et particulière des reptiles, vol. II, chelonians and crocodilians, 1802, p. 30 (type-locality, Amboyna).

Kinosternon amboinense, Bell, Zool. Jour., vol. 2, 1825, p. 305.

Cistudo amboinensis, Gray, Illustrations of Indian Zoology . . . , 1830, vol. 1, pl. 77; Cantor, Jour. Asiat. Soc. Bengal, vol. 16, 1847, p. 611.

Cuora amboinensis, Gray, Catalogue of the shield reptiles of the British Museum, Testudinata (Tortoises), 1855, pt. 1, p. 41; Günther, The reptiles of British India, 1864, p. 12, p. 4; Gray, Supplement to the catalogue of shield reptiles in the collection of the British Museum, pt. 1, Testudinata, 1870, p. 21, figs.; M. Smith, The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 84-86, plate 1, fig. 4, text fig. 16; Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, 1955, p. 347.

Cyclemys amboinensis, Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 33; The fauna of British India, Ceylon and Burma, 1890, p. 31, fig. 10; Siebenrock, Sitzungb. Akad. Wiss. Wien., Band 112, abt. 1, 1903, p. 343; Zool. Jahrb., Suppl. 10, 1909, p. 503; Flower, Proc. Zool. Soc. London, 1899, p. 614; Boulenger, Fasciculi Malayenses, Zool., vol. 1, 1903, p. 142; A vertebrate fauna of the Malay Peninsula. . . . Reptilia and Batrachia, 1912, pp. 21-22.

Emys couro Schweigger, Prodromi monographiae cheloniorum, pt. I, 1814, p. 46 (type-locality, Java).

Terrapene bicolor Bell, Zool. Jour., vol. 2, 1825, p. 484, pl. 16. Type-locality unknown ("type from America" *ex errore*).

Diagnosis: Carapace depressed in young, tricarinate, usually strongly convex, with an obsolescent keel in adult males and females; plastron as large as opening of carapace, lacking a distinct bridge; axillary and inguinal scales absent or very small; distinct hinge between pectorals and abdominals (hyo- and hypoplastral bones) both lobes being movable, and capable of closing shell completely. Plastron rounded posteriorly, with a feeble median nick; digits fully webbed; sole of foot with numerous small flat scales.

Description of species (No. 1642, EHT-HMS Collection.): Carapace somewhat compressed, high, convex; median dorsal region not depressed or flattened; distinct evidence of a median keel; nuchal scute small, narrow, more than twice as long as wide; anterior vertebral scute wider anteriorly (33 mm) than posteriorly (29.5 mm); length of scale, 33 mm; second vertebral as long as wide; third and fourth distinctly wider than long; last longer than wide; first costal as wide as long; second, third, and fourth wider than long; marginals erect, the subcaudals flaring somewhat; marginals not serrate, lacking notch between subcaudals.

Plastron strongly concave (♂), as wide as opening in carapace; no bridge between plastron and marginals; no distinct axillary or inguinal scales; the space between plastron and marginals with small irregular scutes or divided skin; front section of plastron rounded; a hinge between pectoral and abdominal scutes leaving both parts of plastron movable and capable of closing the openings completely; posterior section of plastron rounded, with a tiny median notch; plastron narrowed at suture between abdominals and femorals; length (in mm) of common sutures of plastral scutes: gular, 30; humeral, 7; pectoral, 32.5; abdominal, 38; femoral, 15; anal, 40.

Head moderately large, snout rather pointed. Skin or head undivided on anterior half, posterior half broken into 2 large scales; area in front of lower tympanic area covered with minute scales; upper jaw and lower jaw each covered with a single scute; no enlarged scute posterior to lower jaw; upper

jaw slightly hooked anteriorly; skin over ear partly broken into scutes; front of arm covered with transverse, enlarged, somewhat imbricating scutes, a row of elongate scales along the dorsal surface; 4 large scales on posterior face of arm arranged transversely. Fingers almost completely webbed; heel with a few enlarged scutes above and below with other enlarged scutes above each toe and finger; underside of hand and foot with numerous rather small, flat scales; paired scutes under tail with enlarged irregular scales at tip. Snout a little shorter than orbit.

Color: Above nearly uniform blackish on carapace; top of head brownish, growing black posteriorly; top of neck gradually becoming gray. A dark-edged yellow stripe runs from neck above and meets its fellow on tip of snout; a broad black stripe below this passes through eye, narrowing and terminating at tip of snout; a broad yellow stripe from neck crosses ear, bisected by a black line from in front of ear to tip of snout, bordered below by a narrow black line. Underside of neck and chin dirty yellowish white.

Plastron and underside of marginals pale yellowish, each marginal with a peripheral black spot. Plastron with a dark olive figure incorporating the more intense black spots on each of the plastral scutes.

Measurements in mm: Length of carapace, 182; width of carapace, 135; depth of carapace, 82; length of plastron, 168; greatest width of plastron, 93.5; width of head, 31.5; length of head, 45.

Variation: The chief differences are those that occur between young and adult specimens. In the young the carapace is rather flattened with a strong vertebral keel and 2 small lateral keels; the laterals are completely lost in the adult, and the vertebral keel is more or less evident. In adults the carapace is much deeper proportionally without trace of dorsal flattening. It is distinctly convex.

The first vertebral scute is broader behind than in front in the young; in the adult they may be the same, front and back, or the front may be wider. The skin on the back of the head may be smooth, unbroken, or there may be a few large scutes indicated.

Distribution: In Thailand the species is widespread in lowland streams, lakes and swamps. Specimens have been taken in the province of Chiang Mai. I presume it is not especially rare. I have seen other specimens, these lacking exact locality data.

Outside of Thailand the species is spread from southern Burma, Indo-China, and Malaya, to the Indo-Australian Archipelago. It reaches the Philippines and Celebes. The type-locality is the Island of Amboyna (Ambon).

Genus **Heosemys** Stejneger

Geoemyda Gray, Proc. Zool. Soc., 1834, p. 100 (type of genus, *Testudo spengleri* Gmelin); Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History), 1899, p. 186; The Fauna of British India, including Ceylon and

Burma. Reptilia and Batrachia. 1890, p. 24 *(part.)*; Stejneger, Proc. Biol. Soc. Washington, vol. 15, 1902, p. 238; Siebenrock, Zool. Jahrb., Suppl., Band 10, 1909, p. 494 *(part.)*.

Geomys Bonaparte, Tavola Analitica dei Chelonii 1836, p. 36.

Nicoria Gray, Catalogue of the shield reptiles in the collection of the British Museum, Part 1, Testudinata (tortoises), 1855, p. 17; Boulenger, Catalogue of the chelonians. . . . 1899, p. 118; The Fauna of British India. . . . 1890, p. 26 *(part.)*.

Melanochelys Gray, Proc. Zool. Soc. London, 1869, p. 187 (type of genus, *Geoemyda trijuga* Schweigger).

Chaibassia Theobald, Descriptive catalogue of the reptiles of British India, Calcutta, 1876, p. 6 (type of genus, *Geoemyda tricarinata* Blyth).

Heosemys Stejneger, Proc. Biol. Soc. Washington, vol. 15, 1902, p. 238 (type of genus, *Geoemyda spinosa* (Bell)).

Diagnosis: Skin of head hard, smooth or broken into scales posteriorly. Plastron widely united to carapace by a suture; axillary and inguinal buttresses present, extending to outer margins of costal plates; entoplastron usually intersected by the humeropectoral suture; no median ridge on alveolar surface of jaws; neural plates, except first, narrowed posteriorly. Skull with or without a bony temporal arch (variable during lifetime).

This genus is cosmopolitan, occurring also in the Western Hemisphere in Central and South America. Annandale (1923a) and M. A. Smith (1931a) have shown that one character in the genus, formerly used for generic separation, is useless. This was the presence or absence of a complete temporal arch. Both of these authors show that although at some stage the arch may be present it begins to become thinner and narrower. Then the quadratojugal may disappear; later the postorbital, and the jugal, and only a slight process may mark where these bones were present. This is indeed a curious reversal of the evolutionary process, or as called by Smith, *devolution*.

Two species of *Heosemys* are certainly endemic in Thailand, *H. spinosa* (Bell), and *H. grandis* Gray.

Key to Species of *Heosemys* in Thailand

1. Anterior margin of the shell serrated; second vertebral scale as broad as second costal, much broader than long ..... *spinosa*
2. Anterior margin of shell not serrated; the second vertebral narrower than second costal, not or but slightly broader than long ..... *grandis*

Heosemys spinosa Bell, *in* Gray

Emys spinosa Bell, *in* Gray, Illustrations of Indian Zoology, 1830, pt. 1, pl. 6; Synopsis reptilium or short descriptions of the species of reptiles, 1831, p. 20 (type-locality, Penang).

Geoemyda spinosa, Gray, Proc. Zool. Soc., 1834, p. 100; Illustrations of Indian Zoology, 1835, vol. 2, pl. 57; Boulenger, Catalogue of the chelonians rhynchocephalians and crocodiles in the British Museum, 1889, p. 137; Fauna of British India, including Ceylon and Burma. Reptilia and Batrachia. 1890, p. 35; S. Flower, Proc. Zool. Soc. London, 1899, p. 614; Ridley Jour. Straits Branch Roy. Asiatic Soc., No. 32, 1899, p. 185; Boulenger, Fasciculi Malayenses, pt. 1, 1903, p. 144; M. Smith, The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 91-94, figs. 17a, b; Mertens and Wermuth, Zool. Jahrb. (Syst.), Jena, 1955, Band 83, Heft 5, p. 353.

Heosemys spinosa, Siebenrock, Zool. Jahrb. (Syst.), Jena, 1909, Suppl. 10, p. 506.

Diagnosis: Tail short, lacking elongated spines at its base; no bony temporal arch. Carapace with single median keel; upper jaw notched. Anterior margin of shell serrated; second vertebral shield at least as broad as second costal, much broader than long.

Description of species: A medium sized turtle with arched carapace in young, bearing a strong median keel, and each costal scale bearing a small rather sharp spine near its posterior edge. Carapace about as broad as long, strongly serrate all around carapace; marginals terminating in a dull spine, or sometimes with a double spine. Nuchal small.

The carapace of adult animal much depressed, with a flattened vertebral region and a well-defined keel; costal spines usually lost. Margin of carapace less strongly serrate; first vertebral scute broader than long, narrowed anteriorly; the following vertebrals all much wider than long, equally or nearly as broad as costals. Plastron as long as carapace, angled rather than rounded posteriorly; posterior lobe of plastron as well as anterior somewhat narrower than opening of carapace; posterior lobe strongly notched. Longest median suture of plastral scutes between abdominals or pectorals (nearly equal but usually the former); length of other sutures diminishes in following order: femoral, humeral, gular, anal. Plastron attached directly to marginals, bridge more than a third length of plastron.

The head relatively small; snout about as long as orbit of eye, terminally truncate. Edge of jaw with two denticulations. No temporal arch in skull. Skin of head partially squamate posteriorly.

Arms with enlarged, more or less imbricating scales, on anterior face; legs more or less club-shaped in adults, less so in young, with enlarged scales on anterior and posterior margins. Under surface of foot scaled. Fingers half webbed, toes less so. Back of thighs and part of anal area with small scales or conical tubercles. (Description from literature.)

Color: Generally brownish with a median lighter line or streak. Plastron and underside of marginals yellowish with radiating lines. Head grayish or brownish with yellow spot near the tympanum; occasionally, specimens with yellowish longitudinal lines. Small yellowish spots on limbs.

Measurements in mm: Total length, 225; width, 162; height of shell, 82.

Remarks: In Thailand the species is distributed chiefly in the rivers of mountainous areas in the peninsula. It feeds largely on aquatic vegetation.

The species is also known from southern Burma, Malaya, and the more western islands (Borneo and Sumatra) of the Indo-Australian Archipelago.

Heosemys grandis Gray

(Fig. 4)

Geoemyda grandis Gray, Ann. Mag. Nat. Hist., ser. 3, vol. 6, 1860, p. 218 (type-locality, Cambodia); Günther, Reptiles of British India, 1864, p. 19, pls. 1, 2; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural

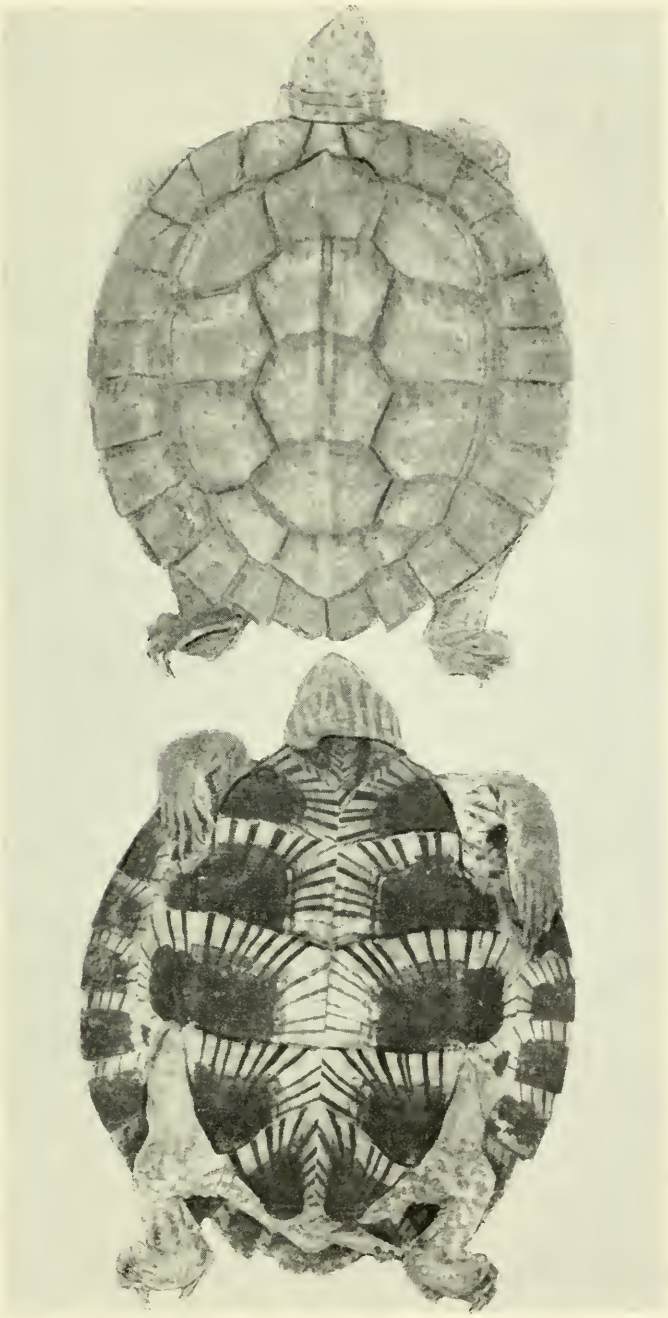

Figure 4. *Heosemys grandis* Gray. Chulalongkorn Univ. No. 1590, Bhetong, Yala, Thailand. Length of carapace, 110 mm; width of carapace, 104. Upper figure, dorsal view; lower, ventral view.

History), 1889, p. 138; Fauna of British India including Ceylon and Burma, Reptilia and Batrachia, 1890, p. 25, figs. 7 & 8; M.A. Smith, The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia, vol. 1, Loricata, Testudines, 1931, pp. 101-103, figs. 20, 21; Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, 1955, p. 350.

Diagnosis: Anterior margin of shell not serrate; second vertebral not or scarcely broader than second costal. No bony temporal arch.

Description of species (largely from no. 1641, Bhetong, Yala, Thailand): Carapace subcircular, about as broad as long, somewhat depressed in young but with median keel. Shell arched in adults; anterior edge of carapace not serrate; posterior edge somewhat serrate and slightly bent down. Eleven marginals on each side, a pair of supracaudals and a single small, but well-defined nuchal.

Five vertebral shields, first as long as wide (or sometimes longer), narrowed somewhat anteriorly, the shields following about as long as broad, not or but slightly narrower than costals; plastron nearly as long as carapace, extending slightly farther forward than carapace but shorter posteriorly; posterior section narrower than shell opening, a little shorter than bridge. Sutures of plastron vary, the longest between abdominals, the shortest between humerals or gulars. Axillary and inguinal shields present.

Head not especially small; snout as long as the diameter of eye, scarcely reaching beyond mouth; upper jaw bicuspid. No bony temporal arch. Skin of posterior part of head more or less broken into irregular shields. Enlarged scales on front of arms and posterior part of legs; digits webbed; tail short.

Color: Variable, but usually shell brownish above with slight or practically no variegation; ventrally, shields pale yellowish, each with a large dark (blackish) area, with numerous marks radiating from posterior part of shield. Ventral part of marginals similarly marked. Exposed skin of limbs greenish gray with flecks or vermiculations. Top of head greenish gray with occasional pinkish marks.

Measurements in mm of young: Total length of carapace, 110; width of carapace, 104; head width, 20.

Distribution: The species occurs along the Burma (Tenasserim)-Thai border ranging as far north as Pegu in Burma. Most Thai specimens, however, are from peninsular areas. It is known to occur in the northern states of Malaysia.

The species is probably the largest Asiatic member of the genus. Malcolm Smith reports a specimen from the Burmese-Thai border having a carapace 435 mm long.

Genus **Malayemys** Lindholm

Damonia (*non*-Robineau-Desvoidy) *(part.)* Gray, Proc. Zool. Soc. London, 1869, p. 193 (type of genus, *D. macrocephala*).

Malayemys Lindholm, Zool. Anz., Band 97, Dec. 1, 1931, no. 1, 2, p. 29 (new name for *Damonia*, Gray).

Diagnosis: Second neural plate short-sided in front, third octagonal, fourth and fifth short-sided behind; plastron extensively united to carapace by suture, with strong axillary and inguinal buttresses which extend to outer extremities of costal plates. Entoplastron anterior to humeropectoral suture; skull with bony temporal arch formed chiefly of quadratojugal, which contacts the maxillary bone; jugal small, almost or completely excluded from orbit. Alveolar surface of jaws very broad, without median ridge; bony choanae on a level with posterior margin of orbit. Skin of hinder part of head divided into small shields. Digits fully webbed. Tail very short.

Only a single species is recognized.

Malayemys subtrijuga Schlegel and S. Müller *in* Temminck

(Fig. 5)

Emys trijuga (not of Schweigger) Schlegel, Fauna Japonica. . . . Reptilia, 1833, p. 64 (type-locality, Java).

Emys subtrijuga Schlegel and S. Müller, *in* Temminck, Verh. Nat. Ges. Ned. Indie, Rept., 1844, p. 30.

Damonia subtrijuga, Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 94; Flower, Proc. Zool. Soc. London, 1899, p. 610; M. Smith, The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, Mar. 1931, pp. 105-106, figs. 22 (skull), 23 (shell).

Geoclemys subtrijuga, Siebenrock, Zool. Jahrb. Jena, Suppl. 10, 1909, p. 476.

Geoclemys macrocephala Gray, Proc. Zool. Soc. London, 1859, p. 479, pl. 21 (type-locality, Siam).

Emys nuchalis Blyth, Jour. Asiat. Soc. Bengal, vol. 32, 1863, p. 82 (type-locality, Java?).

Damonia oblonga Gray, Ann. Mag. Nat. Hist., ser. 4, vol. 8, 1871, p. 367 (type-locality, Batavia).

Damonia crassiceps Gray, Supplement to the catalogue of the shield reptiles in the collection of the British Museum, pt. 1, Testudinata, 1870, p. 43 (type-locality, China).

Malayemys subtrijuga, Lindholm, Zool. Anz., Leipzig, Bd. 97, 1931, p. 29 (new name for *Damonia,* preoccupied); Mertens und Wermuth, Zool. Jahrb. (Suppl.), Band 83, Heft 5, 1955, p. 360.

Diagnosis: Tricarinate carapace; keels retained more or less throughout life; lateral keel not extending across fourth costal; head large; yellow lateral stripes on head and neck; carapace brown with dark spots on marginal sutures, strongly pronounced on their ventral surface and spreading over half of the scute; plastral scales each with a large dark area; no scutes on tail; back of head with 15-20 small scales.

Description of species (from No. 33675, Bangkok): Medium-sized, carapace length reaching 210 mm; carapace moderately arched, somewhat depressed; discontinuous keels evident, tending to form slight knobs at posterior point of scales; nuchal scale relatively large, more than one and a half times as long as wide, projecting slightly beyond front border of adjoining marginals; measurements in mm of dorsal scutes (length x width): vertebrals, first, 42 x 34 mm, wider behind than anteriorly; second, 37 x 37 mm; third, 34 x 43 mm; fourth, 31 x 49 mm; fifth, 40 x 51 mm; costals: first, 53 x 52 mm; second, 38 x 60 mm; third, 40 x 58 mm; fourth, 40 x 41 mm (measurement

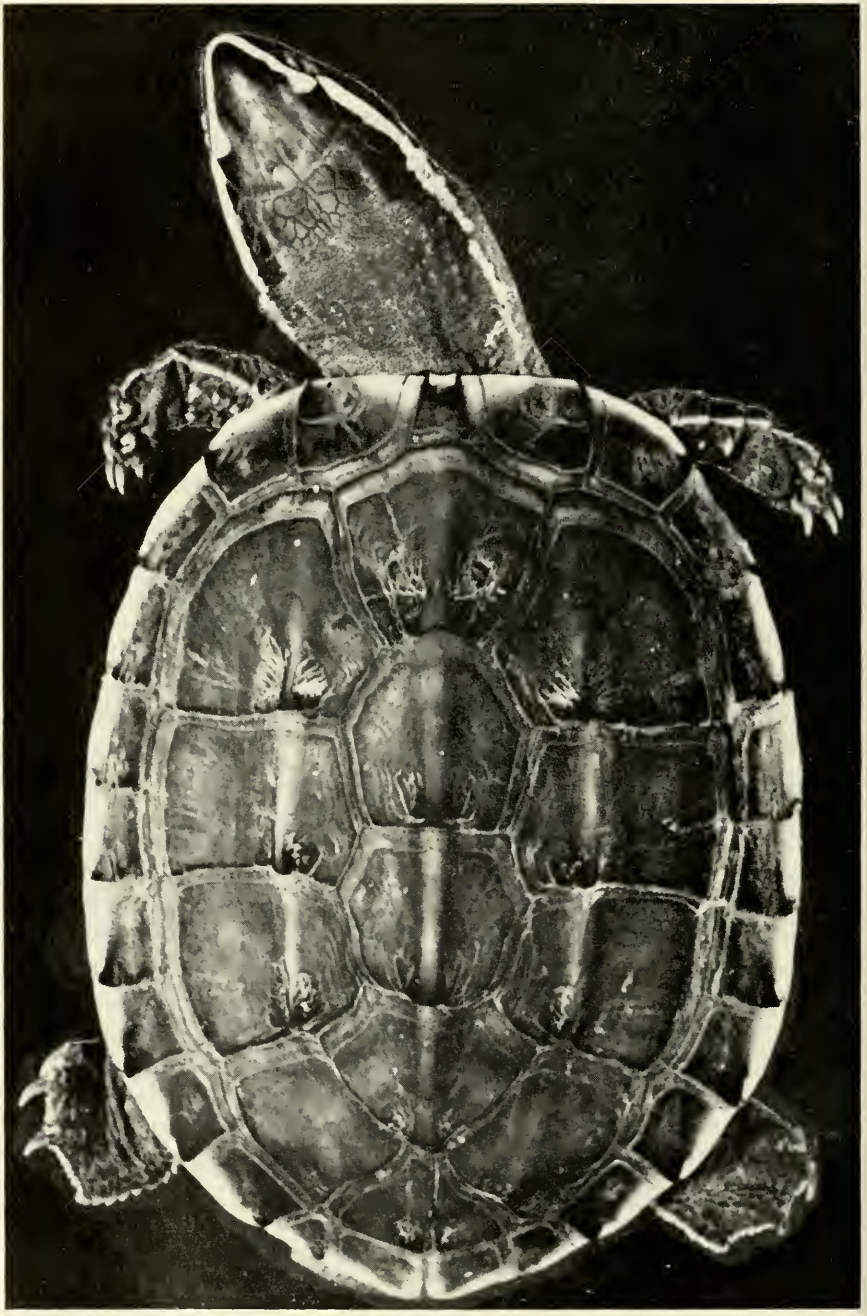

FIGURE 5. *Malayemys subtrijuga* (Schlegel and Müller *in* Temminck), Chulalongkorn Univ. No. 33675. Bangkok, Thailand. Carapace length, 204 mm.

made at widest [or longest] part of scale); supracaudal scales tectiform, notched slightly behind. Plastron distinctly shorter than carapace, truncate anteriorly, outer tip of each gular pointed, the point short, directed forward; strongly notched on posterior border; a broad bridge; plastral edge not or scarcely angular; length of bridge (67 mm) a little longer than posterior lobe of plastron (61 mm). Measurements in mm of median sutures of plastral scutes: gular, 19; humeral, 20; pectoral, 24; abdominal, 46; femoral, 25; anal, 24.5. Axillary and inguinal scales relatively large.

Front face of forearm with transversely widened scutes, usually separated by smaller scales not imbricating; upper edge of arm with row of 4 large scales; back face of forearm with a row of scales partly crossing arm transversely and 1 or 2 others adjoining these; toes fully webbed, claws moderate; leg with a double row of small scales bordering outer posterior edge of foot; posterior region of thighs and area above tail with a few conical scales surrounded and separated by fine, sharply pointed scales, some of these bearing 2 or 3 sharp spines, all very small, almost microscopic; under tail 2 rows of flat scales diverging from tip, each scale bearing on its posterior edge 3 to 5 sharply pointed spines. Soles of feet and palms of hand with small rounded juxtaposed scales.

Head large, skin of top smooth and undivided anteriorly, posterior part broken up into 4 or 5 rows of small scales which extend on sides of head, larger ones anteriorly, smallest posteriorly. A very large scute behind eye, bordering upper jaw scute; snout projecting beyond mouth (6 mm); upper jaw notched but not "toothed" or hooked; scute on lower jaw followed by 2 somewhat enlarged scales, 1 on each side.

Color: Above, carapace dark brown of varying shades, the scales lighter brown at periphery; marginal scales with some blackish areas near sutures, but on ventral side of marginals triangular black spots; plastron pale yellow, each scute with a large black or black-brown area; pectorals and abdominals each with 2 spots (the second one being on the bridge); well-defined black marks on axillary and inguinal scutes. Head black; an ivory-white line from tip of snout above eye and ear area to base of neck; a second ivory line from behind nostrils down below eye, crossing jaw angle, more or less continuous with a line running back on neck; two parallel lines from nostrils to mouth, more or less continuous with lines crossing lower jaw; a small line from lower jaw to throat; soft parts olive-gray; limbs darker on upper surfaces.

Measurements in mm: (see Tab. 1).

Variation: In the young the keels are more distinct and there is a broken line of dots crossing the temporal area (No. 1625). The black marginal lines along the sutures pass below, where they may be slightly wider. The posterior part of the carapace is without or with only a suggestion

TABLE 1. Measurements in mm of *Malayemys subtrijuga*.

Number*	34484	33675	1625
Length of carapace	183	204	103
Width of carapace	146	146	94
Depth of shell	80	81	44
Length of plastron	159	163	101
Width of plastron at bridge	118	120	78
Width of anterior lobe	91	83	52.5
Width of posterior lobe	82.5	78	51
Width of head	47	42	26
Tail	8	13	9
Orbit	13	11.5	8
Snout	11.3	10	7.3

* 34484, Pattani; 33675, Chiang Mai; 1625 Ang Hin, Chon Buri.

of serration. The first vertebral is distinctly wider anteriorly than behind, the reverse of the condition in the adult; the projection of the nuchal is an individual character. This does not obtain in the other specimens examined. The color of the head may be brown, chestnut or dark olive in the adult.

Distribution: The species is probably to be found over the entire country of Thailand. Some 20 specimens were taken in the city of Chiang Mai in a small pond near the Railway Hotel. I have specimens from Pattani, in the southern part of peninsular Thailand, from Bangkok and from Chon Buri, southeastern Thailand.

Outside of Thailand it has been found in Indo-China. It is the common turtle of the klongs of Bangkok.

Remarks: The species is easily kept in small ponds. It feeds largely on small water animals, preferring molluscs, insects, and worms.

Genus **Hieremys** M. A. Smith

Hieremys M. A. Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 50 (type of genus, *Cyclemys annandalii* Boulenger); Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 357.

Diagnosis: Plastron united to the carapace by sutures. Temporal arch incomplete, most of the quadratojugal being absent. Alveolar surfaces of jaws not narrowed, lacking median ridge. Skin of posterior part of head not forming scutes.

The second neural plate hexagonal, with its short side on anterior border. The plates following have their short side posteriorly. Digits completely webbed.

The genus is known to contain only a single species, *Hieremys annandalii*.

Hieremys annandalii (Boulenger)

(Fig. 6)

Cyclemys annandalii Boulenger, Fasciculi Malayenses, Zoology, vol. 1, 1903, p. 142, pls. 7, 8

(type-locality, "Jalor, Patani"): A vertebrate fauna of the Malay Peninsula. . . . Reptilia and Batrachia 1912, pp. 19-20, fig. 6.

Hieremys annandalii, M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, 1916, p. 50; M. Smith, The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, Mar. 1931, pp. 107-109, figs. 24, 25; Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, 1955, p. 357.

Diagnosis: Large turtle (carapace length to 450 mm); carapace much longer than broad, with median keel more or less retained in old adults; normally 5 vertebrals (rarely 6); hind lobe of plastron shorter than length of plastral bridge; longest median plastral suture between abdominals; relatively large axillary and inguinal shields; shortest median suture between humerals; tail short; head with narrow stripe from snout above eye and ear to neck.

Description of species (from No. 1684, Bangkok): Carapace with a single keel (rather low), convex (but not flattened) dorsally, much longer than wide (251 x 190 mm), posterior rim distinctly serrate, anterior rim almost smooth in adult. Nuchal present, sides nearly parallel to near tip; anterior vertebral wider anteriorly than posteriorly (56-40 mm), its length 47 mm, its posterior edge sinuous with a median notch; width x length (in mm) of second vertebral 58 (measured on curve) x 55, with a short anterior median projection; third, 68 x 46, fourth, 62 x 44.5, last, 52 x 38. Costals: first 60 x 58; second, 66 x 45; third, 62 x 55; fourth, 40 x 44. Marginals not or but very slightly reverted; a notch between supracaudals.

Plastron nearly as long as carapace, somewhat angulate at least anteriorly on pectorals, not or scarcely emarginate on anterior end, deeply notched posteriorly; bridge wide, elongate, considerably longer than posterior lobe of plastron; median sutures between plastral scales with the following lengths in mm: gulars, 36; humerals, 19; pectorals, 43; abdominals, 52; femorals, 44; anals, 25. Inguinal large with a row of small scales bordering it behind; axillary also relatively large.

Arms not especially flattened, webbed to base of claws; entire front face from elbow covered with juxtaposed or slightly imbricate transverse scales larger near the upper surface; posterior surface likewise with transverse enlarged scales larger toward the upper part; a single row on upper surface with scales as long as wide; legs more flattened, heel area above and below with transversely widened, somewhat imbricate scales; sole of foot and palm of hand covered with flat juxtaposed scales. Tail short, upper surface of head not divided into scales but somewhat creased; beak with a median and 2 lateral notches; margin of lower jaw with strong denticulations, median ones largest.

Color: Carapace black, nearly uniform; inner edges of marginals on ventral face pale yellow; plastral scales with large blackish areas on pale yellow ground-color; the black area suggests irregular radiating blackish marks; arms and legs dark gray on upper surfaces, lighter gray below.

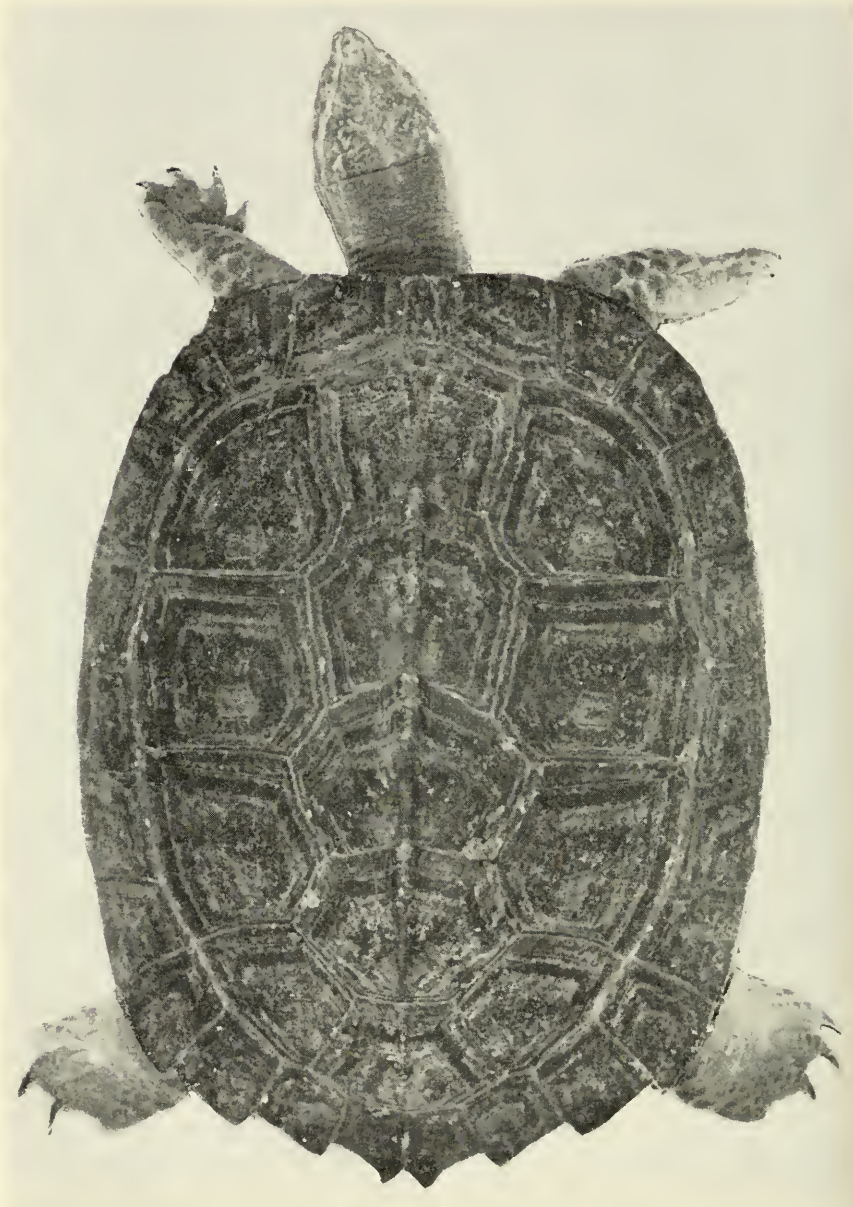

FIGURE 6. *Hieremys annandalii* Boulenger. Chulalongkorn University, No. 1684, Bangkok, Thailand. Carapace length, 242 mm.

Head blackish, flecked or marked with gray. A narrow whitish mark from upper tip of snout, above eye and ear, to side of neck; a broader light line on neck above this, terminating in a triangular spot on temporal region; front of snout and upper jaw whitish; lower jaw whitish with a black mark along jaw angle. Top of neck grayish proximally, darker brownish-black more distally; throat dull white; chin similar with a few darker flecks.

Measurements in mm: Length of carapace, 242; width of carapace, 187; depth of carapace, 93; length of plastron, 230; greatest width of plastron at bridge, 147; width of anterior plastral lobe, 116; width of posterior lobe, 102; length of bridge, 93; length of posterior lobe, 87; width of head, 37; length of head, 56; tail, 27.

Variation: The carapace is more depressed in the young than in the adult, proportionally shorter and with the keel much more distinct. The posterior margin, in the adults, varies. In some the strong juvenile serrations are retained; however, in the oldest specimens the serrations may be obsolete. Occasional specimens have 6 vertebral scales, 1 intercalated between the fourth and fifth. The vertebral scales are broader than long in the young, about as broad as long in the adults, usually narrower than costals; in young specimens the plastron is somewhat angulate. The snout is usually shorter than orbit, projecting somewhat beyond the lower jaw.

The plastron may be entirely black. The soft parts may be greenish gray. In older individuals the dark streaks usually disappear, the head becoming gray with yellowish or greenish vermiculations. The jaws are greenish in many specimens.

Distribution: In Thailand the species is known in the peninsular area and in the central region. Specimens I have examined have been taken chiefly from the river at Bangkok. The species has also been taken in Narathiwat and Pattani Provinces. It is known in Malaya and specimens have been taken in Cambodia.

Remarks: The species readily takes fruit and waterplants and most green garden truck and vegetables. This is their staple diet at the Dusit Zoo in Bangkok. Many may be seen at the Tortoise Temple in Bangkok. Of this Malcolm Smith (1931a) writes: "Numbers of them are usually to be seen in the Tortoise Temple in Bangkok, an honour which they share with *Geoemyda grandis,* a species of much the same size and general external features. No particular form of worship is attached to these tortoises. They are presented to the temple in accordance with the tenets of the Buddhist religion, by which a life saved gains merit for the saver in the next world. Having saved the life of the tortoise the obligation ceases, and no particular care is taken of them in the temple afterwards."

Genus **Notochelys** Gray

Notochelys Gray, Proc. Zool. Soc. London, 1863, p. 177 (type of genus, *Emys platynota* Gray).
Cyclemys (part.), Boulenger, Catalogue of the Chelonians . . . in the British Museum, 1889, p. 129.

Diagnosis: The plastron with a distinct bridge attached to carapace by ligamentous tissue rather than by suture. Hexagonal neural plates with their short side anteriorly. An indistinct, more or less movable hinge between hyoplastron and hypoplastron; entoplastron intersected by the humeropectoral suture. A complete temporal arch, or partial temporal arch if postorbital or quadratojugal is lost. Alveolar jaw surfaces narrowed. Fingers and toes completely webbed. Carapace flattened with a more or less continuous median keel.

Only a single species, *Notochelys platynota* Gray, is known. It has a southeastern Asiatic distribution. It is known to occur in southern Thailand, Cochin China, Malaya, and the Indo-Australian Archipelago. Smith (1931a) reports that the record originally given by Gray for Tenasserim is in error.

I have not encountered this species and the description here included is from the literature.

Notochelys platynota Gray

Emys platynota Gray, Proc. Zool. Soc. London, 1834, p. 54; Illustrations of Indian Zoology, 1834, vol. 2, pl. 57 (type-locality, Sumatra).
Cyclemys platynota, Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 130; The fauna of British India, including Ceylon and Burma. Reptilia and Batrachia. 1890, p. 30; Flower, Proc. Zool. Soc. London, 1899, p. 612.
Notochelys platynota, Siebenrock, Sitzb. Akad. Wiss. Wien, Band 112, 1903, p. 344; Zool. Jahrb., Suppl. Band 10, 1909, p. 504; M. A. Smith, The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 110-111; Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 361.
Cyclemys giebelii Hubrecht, Notes Leiden Mus. vol. 3, 1881, p. 45 (type-locality, Banka, Borneo).

Description of species: A rather small turtle, the length of carapace probably not exceeding 340 mm; slightly wider carapace, relatively flat with a more-or-less developed median keel, sometimes discontinuous; anterior margin serrated in young but not in adults; posterior margin serrate throughout life. Carapace margin with 11 marginals on each side, 2 posterior supracaudals and a small median anterior nuchal. Six (or 7 rarely) vertebral shields, broader than long and narrower than costal shields.

A distinct bridge between plastron and carapace; plastron shorter than carapace and narrower than its opening, truncate or emarginate anteriorly and posteriorly, the length of posterior lobe as great as width of bridge. Longest median suture of plastron between abdominal or pectoral shields; shortest suture between humerals or femorals. Axillary shield small or sometimes absent, inguinal shield relatively large.

The snout about length of orbit, projecting beyond mouth; upper jaw

bearing two cusps. Back part of head with small shields; hands and feet fully webbed.

Color: Color and markings of shell variable. The young usually chestnut brown with 2 dark spots on each vertebral shield, 1 on each costal shield. Adults brown or reddish brown, yellowish on plastron, each shield with a black or brown spot. In very old specimens, areas may be almost completely dark. Head and neck dark, brownish or blackish with yellow streaks, those behind eyes most conspicuous. These markings may be wanting in old specimens.

Dimensions: Malcolm Smith (1931a) reports a specimen with a length of 320 mm; width, 230 mm; height, 92 mm.

Remarks: The species is known to occur in Thailand chiefly in the peninsular portion of the country.

Genus **Siebenrockiella** Lindholm

Bellia (not of Milne-Edwards 1848), Gray, Proc. Zool. Soc. London, 1869, p. 197, type, *Emys crassicollis* (Gray).

Siebenrockiella Lindholm, Zool. Anz., Leipzig, Band 81, Heft 11/12, 1929, p. 280 (type *Emys crassicollis* (Gray)).

Diagnosis: Hexagonal neural plates short-sided in front. Plastron extensively united to carapace by suture with strong axillary and inguinal buttresses which extend to outer extremities of costal plates; entoplastron intersected by a humeropectoral suture. Skull with bony temporal arch, the quadratojugal being in contact with jugal and postorbital. Alveolar surfaces of jaws narrow, without median ridge; bony choanae on level with anterior half of orbits. Skin of hinder part of head divided into small shields. Digits fully webbed. Tail short. From M. Smith (1931a).

Only a single species is recognized in this genus.

Siebenrockiella crassicollis (Gray)

Emys crassicollis Gray, Illustrations of Indian Zoology, 1831, pl. 76; Synopsis reptilium or short descriptions of the species of reptiles, Part 1, *Cataphracta* tortoises, crocodiles and enaliosaurians, 1831, p. 21 (type-locality, Sumatra); Günther, The reptiles of British India, 1864, p. 28, pl. 4; Morice, Coup d'oeil fauna Cochinchine, 1875, p. 63.

Bellia crassicollis, Gray, Proc. Zool. Soc. London, 1869, p. 197; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 981; The fauna of British India. . . . 1890, p. 32; Siebenrock, Zool. Jahrb., Jena, Suppl. 10, 1909, Heft 3, p. 478; Annandale, Rec. Ind. Mus., vol. 11, 1915, p. 194.

Siebenrockiella crassicollis, Lindholm, Zool. Anz., Band 81, Heft 11/12, 1929, p. 280; M. Smith, The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 112-114, fig. 26 and pl. 1, fig. 1; Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 367.

Emys nigra Blyth, Jour. Asiat. Soc. Bengal, vol. 24, 1855, p. 713 (type-locality, Tenasserim).

Pangshura cochinchinensis Tirant, Notes sur les reptiles et les batraciens de la Cochinchine et du Cambodge, Saigon, 1885, p. 15 (type-locality, Cochin China).

Diagnosis: Generic characters. The vertebral shields are narrower poste-

riorly than anteriorly, except fifth. Second with an hemispherical front portion. Five claws on hand, 4 on feet.

Description of species (from No. 1714, Bangkok): Carapace with 3 keels, median distinct; lateral keels better indicated in young; nuchal subtriangular pointed, anteriorly widened, posterior edge concave; first vertebral widened anteriorly, much narrowed posteriorly; second with front edge rounded, much narrowed posteriorly; third a little wider on anterior edge than on posterior; fourth narrowed anteriorly and posteriorly; fifth much narrowed anteriorly, much widened posteriorly, the posterior border concave. Length and width of vertebrals in mm: first, 33 x 25; second, 29 x 33; third, 28 x 33; fourth, 30 x 35; fifth, 36 x 43. Twelve pairs of marginals including supracaudals which are larger than the 3 marginals on each side preceding them; costals wider than long, very much wider than vertebrals.

Carapace somewhat narrowed anteriorly with a rather distinct lateral keel; posterior marginals serrate.

Plastron smaller than opening of shell; a distinct lateral keel terminating on femorals posteriorly, and in a slight rounded lateral projection anteriorly; front edge of plastron truncate, broadly notched with blunt anterolateral points, a semicircular notch behind. Plastron attached to carapace by suture, its greatest width 94 mm; greatest width of carapace, 127 mm; median sutures of plastral elements measure (in mm): gulars, 17.2; humeral, 11.5; pectoral, 25.4; abdominals, 33; femoral, 24; anal, 19. Axillary and inguinal shields present; tail short.

Head broad, rather large, snout shorter than orbit, rounded, and slightly projecting; upper jaw emarginate; posterior surface of head broken into small shields; a narrow strip of granular shields from eye to tympanum and between shield of lower jaw and tympanum; diameter of tympanum equal to that of orbit.

Arms with 5 clawed fingers, fully webbed; front face of lower arm with transversely widened subimbricate shields; upper arm surface with a row of enlarged scales, posterior face with 3 enlarged shields and about 12 on palm somewhat enlarged.

Foot fully webbed; 4 toes bearing claws, outer without claw. On upper anterior surface of foot 4 or 5 tubercular shields, not touching each other; heel with transversely widened scales on front and posterior face of leg.

Color: Carapace black above, nearly uniform; plastron light horn-color with large blackish areas on each plastral scute; anals nearly entirely dark; underside of marginals black and yellowish. Arms and legs blackish; upper surface of tail blackish.

Head with an indistinct light area behind eye and on tympanum; edge of upper jaw yellowish; remainder of upper side of head black. Chin and throat dirty whitish.

Measurements in mm: (see Tab. 2).

Table 2. Measurements in mm of *Siebenrockiella crassicollis* (Gray).

Number*	1713	1714	1715	1716
Sex	♂	♂	♂	♀
Carapace length	170	196	176	182
Carapace width	129	143	136	142
Plastral length	129	156	143	155
Plastral width, greatest	94	108	105	109
Greatest width of posterior lobe	73	79	76	85
Tail length	13	16	16	13
Width of head	35.5	39	36.5	41

* All from Bangkok.

Variation: No. 1715 has the last vertebral split on one side thus making 5 costals on the left side. This specimen is black on the underside save for a few small yellowish spots on marginals and a rather large continuous yellowish area on the middle of the plastron. One of the specimens has the skin on the crown of the head as well as that of the posterior part divided into small scutes. The lateral plastral keel is more poorly developed in the female specimen. The head markings differ in being more distinct and of a yellowish-white color, despite the fact that it appears to be an old specimen. The carapace tends to be narrowed anteriorly, probably less so in the female.

Distribution: In Thailand the species is common in the rivers and at least in larger ponds. Since it is in northern Malaya and Tenasserin in Burma, one would expect to find it throughout the peninsular area. It is known in Sumatra and Borneo.

Genus **Batagur** Gray

Batagur Gray, Catalogue of the shield reptiles in the collection of the British Museum, Part 1, Testudinata (tortoises), vol. 1, 1855, p. 35, pl. 16; Supplement to the catalogue of shield reptiles in the collection of the British Museum, Part 1, Testudinata 1870, pp. 51-53, fig. 18 (type of genus, *Emys baska*).

Tetraonyx Lesson, Illustrations of Zoology, 1832, pl. 7 (type, *T. longicollis*). (Not of Latreille, 1809.)

Diagnosis: "Neural plates elongate hexagonal, short-sided in front. Plastron extensively united to carapace by suture, with extremely developed axillary and inguinal buttresses which extend nearly to neural plates. The former connected with first rib; entoplastron anterior to humeropectoral suture. Skull with a bony temporal arch, the quadrato-jugal being in contact with jugal and postorbital; bony alveolar surface of jaws very broad with two strongly denticulated ridges. Digits fully webbed with 4 claws only. Tail very short, not longer proportionately in the young than in adults. A single species." From M. A. Smith (1931a).

Batagur baska Gray

(Fig. 7)

Emys baska Gray, Illustrations of Indian Zoology, pt. 4, pl. 8, 1830 (vol. 1, pl. 75); Synopsis reptilium or short descriptions of the species of reptiles, Part I, Cataphracta, tortoises, crocodiles, and enaliosaurians, 1831, p. 24 (type-locality, India).

Batagur baska, Gray, Catalogue of the shield reptiles in the collection of the British Museum, Part I, Testudinata (tortoises), 1855, p. 35, pl. 16; Günther, Reptiles of British India, 1864, p. 37, pl. 3; Boulenger, Catalogue of the chelonians . . . in the British Museum 1889, p. 61; Fauna of British India. . . . 1890, p. 38; Siebenrock, Zool. Jahrb., Suppl. 10, Heft 3, 1909, p. 456; M. A. Smith, Fauna of British India. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 134-135, pl. 1, fig. 2; Mertens and Wermuth, Zool. Jahrb. (Syst.), Band 85, Heft 5, 1955, pp. 341-342.

Emys batagur Gray, Synopsis reptilium, 1831, p. 23; Illustrations of Indian Zoology, vol. 2, 1834, pl. 59 (type-locality, India).

Tetraonyx longicollis Lesson, Illustrations of Zoology, 1832, pl. VII (type-locality, Pegu); Anderson, Anatomical and Zoological researches and zoological results of the Yunnan Expeditions, Reptilia and Amphibia, 1879, p. 77.

Emys tetraonyx Schlegel, Fauna Japonica, 1834, p. 43 (substitute name for *longicollis*).

Tetraonyx lessoni Duméril and Bibron, Erpétologie Générale, vol. 2, 1835, p. 338, pl. 16 (substitute name for *E. batagur*).

Tetraonyx affinis, Cantor, Catalogue of Malayan Reptiles, 1847, p. 6 *(part.)*.

Diagnosis: Characters of the genus.

Description of species (from literature): A large species, carapace reaching half a meter in length with a width of about 440 mm. Carapace smooth, without a keel, somewhat flattened; nuchal shield present, broader than long; marginals not typically serrate; vertebrals variable in size and proportions, second and third about equal, and equal, in general, to the costals. Plastron smaller than opening of carapace, truncate anteriorly and with a posterior notch; bridge wider than length of posterior lobe. Plastral sutures vary, the abdominal sutures longest, gulars shortest. A large inguinal shield, axillary smaller.

Snout projecting, and somewhat turned up at end; skin of occipital region broken into scales. Neck superficially appears to be covered with fine scales. Shell brownish olive to olive-green, whitish or yellowish below. The color may vary during the breeding season.

Measurements in mm: Malcolm Smith (1931a) gives the measurements of a specimen as follows: Length, 590; width, 430; height, 210.

Remarks: This is probably the largest of the Asiatic hard-shelled aquatic turtles. It is reported that they are often seen in large numbers along river banks in India. Smith (1931a), states, "It inhabits estuaries, deep, slow-flowing rivers and canals. They lay from the beginning of January or a little earlier until the end of February or beginning of March. Every day, quite irrespective of the state of the tide, the tortoises come out of the sea and sun themselves on the sand from 2 P.M. till dark. They assemble in herds of from one hundred to five hundred lying quite close to one another. Every night some of them lay eggs, between 10 and 30 in number, in the sand of the beach, digging a hole for them from one and a half to two feet deep above

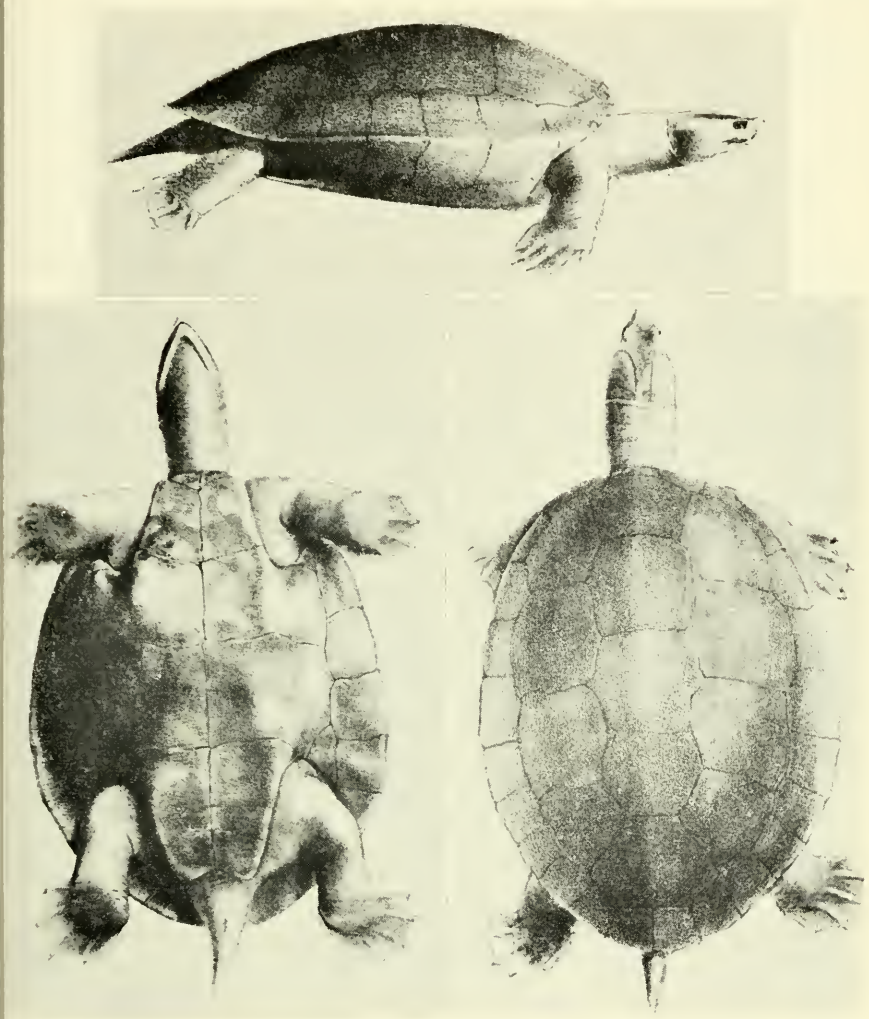

Figure 7. *Batagur baska* Gray. From Gray, "Catalogue of the Shield Reptiles, etc.," 1855, Pt. I, pl. 16.

the influence of the tides. On no consideration will the tortoises allow themselves to be approached: directly they wind a human being they disappear into the sea."

The period of incubation is said to be about 70 days. Altogether 50 to 60 eggs are laid by each female. They are deposited in 3 batches over a period of about 6 weeks time.

The species in Thailand would appear to be much less numerous than in India since they are not known to occur in numbers anywhere.

Smith's (1931a) plate 1, fig. 2, gives a splendid figure of the head, lateral view.

Family Testudinidae Gray

Testudinidae, Gray, Ann. Philos., ser. 2, vol. 10, 1825, p. 210.

Head and neck retractile; limbs somewhat club-shaped; a nuchal plate with riblike process (the scale, however, may be absent as in *Testudo elegans*); plastral and marginal shields not separated on sides. Nine bones in plastron.

Skull with a bony temporal arch; auricular cavity closed posteriorly by quadrate; temporal region not roofed by bone; digits 4 or 5; odoriferous musk glands absent.

The members of this family are typically terrestrial animals; apparently none has become aquatic. They are widespread on earth, the largest ones persisting on the Galapagos of the eastern Pacific Ocean, and on the Seychelles and Aldabra of the Indian Ocean. They are absent in Australia and New Guinea.

These turtles, at least certain of the larger species, are reputed to live to an age in excess of one hundred years. *Testudo leithi* of Egypt is the midget of the family, an old adult having a carapace usually less than 130 mm in length. Of the 4 known genera of the family, only the genus *Testudo* is known to occur in Asia.

Genus Testudo Linnaeus

Testudo Linnaeus, Systema Natura, ed. 10, 1758, p. 197 (type of genus, *Testudo graeca*=*T. ibera* Pallas).

Indotestudo Lindholm, Zool. Anz., Band 81, Heft 11/12, 1929, p. 285 (type of genus, *Testudo elongata*).

Diagnosis: Neural plates hexagonal, short-sided behind or alternately tetragonal or octagonal; costal plates alternately narrower and wider; plastron extensively united to carapace by suture with short axillary and inguinal buttresses which do not reach or just reach the costal plates; alveolar surface of upper jaw with a more or less well-developed median ridge. Choanae on a level with anterior half of orbits. Limbs more or less cylindrical. Legs club-shaped, partly covered with large bony scutes; digits short, unwebbed. Tail short. (Data from M. Smith, 1931a, p. 137.)

There are 3 species of this genus recognized as occurring in Thailand. They may be distinguished by the following key:

Key to Thailand Species of *Testudo*

1. Supracaudal shield single. Nuchal present (rarely absent); a broad suture between pectoral shields, equal to or larger than that be-

tween humerals; shell greenish yellow on carapace and plastron, each shield with a black spot. ..... *elongata*

Supracaudal shield double 2

2. Pectoral shields forming a median suture but shorter than that between other plastral scales; plastron not longer than carapace; nuchal scale rather large, triangular; shell light-brown often with radiating marks especially on plastron; dorsal part of carapace flat, the costals and some vertebrals concave ..... *impressa*

Pectoral shields widely separated; plastron longer than carapace; blackish- to dark-olive, the shields with horn-colored spots ..... *emys*

Testudo elongata Blyth

Testudo elongata Blyth, Jour. Asiat. Soc. Bengal, vol. 22, 1853, p. 639 (type-locality, Tenasserim); Gray, Proc. Zool. Soc., London, 1856, p. 181, pl. 9; Anderson, Zool. Res. W. Yunnan, 1879, p. 706; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the collection in the British Museum, 1889, p. 173; Fauna of British India, . . . including Ceylon and Burma, 1890, p. 20; Siebenrock, Sitzb. Akad. Wiss, Wien, 112, 1903, p. 346; Annandale, Rec. Ind. Mus., vol. 11, 1915, p. 347; M. Smith, Fauna of British India, . . . vol. 1, 1931, pp. 141-143, fig. 29; Mertens and Wermuth, Zool. Jahrb. (Syst.), 1955, Band 83, Heft 5, p. 377.

Testudo parallelus Annandale, Rec. Indian Mus. vol. 9, 1913, p. 76 (type-locality, Chaibassa District, Chota Nagpur).

Diagnosis: Carapace elongate, reaching a length of about 300 mm. Generally yellow above and below, with large dark spots or flecks on dorsum. Larger dark spots on marginal scales. The supracaudal scale single. Top of head with symmetrical scales.

Description of species: Body strongly arched, length of shell about 1.66 times its width, 2.6 times it height; carapace flattened dorsally in adults; posterior and anterior borders of carapace bent down, then slightly reverting. Marginals somewhat serrate in young, not or scarcely so in old specimens.

Head of average size; well-defined pair of prefrontal shields; frontal shield single; occipital shield small; dorsolateral and lateral series of scales unequal, some considerably larger than others. Upper jaw tricuspid, the horny edge of jaw slightly denticulated. Nuchal shield elongate; first vertebral shield as long as broad, following ones broader than long; supracaudal somewhat recurved.

Arm with imbricating scales along outer part. Posterior part of foot with enlarged scales; enlarged scales on posterior part of thigh. Tail curving, ending in a large scale.

Carapace with an elongate nuchal (rarely absent); 5 vertebrals, all broader than long except first; 2 supracaudals, incurving. Plastron large, truncate anteriorly, notched posteriorly. Longest plastral suture between abdominals, shortest between anal pair, which may be completely separated. A small axillary and a larger inguinal shield.

Color: Carapace and plastron dull greenish or greenish yellow; a dark

spot on each scute of carapace, those on vertebrals small, irregular, those on marginals much larger; head greenish yellow; arms and legs with small dark spots.

Measurement in mm: Total length 275; width, 165; depth, 105 (from Malcolm Smith, 1931a).

Remarks: The nuchal shield may be absent. This form is wide-spread from northeastern India east to Cambodia and Vietnam, and south to upper Malaya (Penang). It is not rare in Thailand along the Burmese border.

These large terrestrial tortoises are usually found in hilly or mountainous areas, inasmuch as they are hunted as food in lower cultivated areas. In my own collecting, in large part done in lowland, I have never found a specimen.

The species is known chiefly from the Thailand-Burma border. If present in northern and eastern Thailand it must be much rarer.

A living specimen is pictured by Dr. Boonsong Lekagul (1966, p. 58). Two subgenera have been proposed that involve Thai species. Thus *Testudo emys* and *T. impressa* are in the subgenus *Manouria* and *T. elongata* has been placed in the subgenus *Indotestudo*. See Williams (1952).

Testudo emys Schlegel and S. Müller

Testudo emys Schlegel and S. Müller *in* Temminck, Verh. Nat. Gesch. Ned. Ind., Rept., 1844, p. 34, pl. 4 (type-locality, Sumatra); Anderson, Proc. Zool. Soc., 1872, p. 132-144, figs. 1 to 8; Boulenger, Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum, 1889, p. 158 *(part.)*; The fauna of British India, . . . Reptilia and Batrachia, 1890, p. 22; Flower, Proc. Zool. Soc. London, 1899, p. 616; Siebenrock, Zool. Anz., vol. 30, 1906, p. 583; Zool. Jahrb., Jena (Suppl), 10, Heft 3, 1909, p. 519; M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 2, no. 2, 1916, p. 149 (Khao Wang Hip, Nakhon Si Thammarat); *idem*, vol. 4, no. 4, July 25, 1922, p. 205; Mell, Arch. für Naturgesch., Band 88 (10), 1922, p. 114. Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 377.

Manouria fusca Gray, Proc. Zool. Soc. London, 1852 (1854), p. 134 (type-locality, Singapore).

Manouria emys, Tirant, Notes sur les reptiles et les batraciens de la Cochinchine et du Cambodge, 1885, p. 12.

Testudo phayrei Blyth, Jour. Asiat. Soc. Bengal, vol. 22, 1853 (type-locality, Arakan, Tenasserim, Burma).

Diagnosis: Large species reaching a carapace length of 470 mm, a width of 340, mm, a depth of 195 mm. Carapace somewhat flattened in older specimens; part of anterior and posterior marginal shields recurved, lateral marginals vertical; pectoral shields widely separated from each other; 2 supracaudals. Abdominal scutes largest, suture between them nearly double other median plastral sutures; usually 2 inguinal shields; a group of subconical scales projecting from thighs posteriorly.

Description of species (from a living specimen in the Dusit Zoological Gardens, Bangok): Carapace broadly arching, dorsal surface somewhat flattened; part of shields concave, especially the posterior costals and some marginals; some anterior and posterior marginals recurved somewhat, more or less serrated; nuchal shield well developed, a little longer than broad; 24

marginals, lateral ones standing vertically; vertebral and costal scales broader than long; transverse suture between first 2 vertebrals tending to curve forward; between second and third, suture nearly straight; between third and fourth, suture sinuous with a median forward curve; between fourth and fifth, straight; supracaudal scale divided, curving downward sharply, not or scarcely notched.

Plastron a little longer than carapace; a small axillary and two inguinal scutes; notch between gular scales; humerals broadly in contact with abdominals thus separating pectorals by a distance of 123 mm. Abdominal scales very large, length of suture between them nearly twice that of other plastral shields; a wide notch between anal shields; front end of plastron extending beyond carapace.

Head moderately large, jaw not or only slightly hooked; top of head with a very large frontal scute preceded by 2 pairs of smaller scutes, and followed by a considerable number of smaller, more or less symmetrical scutes. Arms club-shaped, compressed, with 5 clawed digits, anterior (or outer if arm is folded) surface covered with thickened imbricate scutes arranged in several rows, but not entirely surrounding arm. Legs thickened, "club-shaped," with 4 clawed digits; foot somewhat rounded with 10 or 12 enlarged thickened bony scutes on sole of foot, 1 or 2 at posterior edge subconical; area on heel and about ankle with enlarged imbricating scales; scaleless area on posterior surface of thigh and a group of enlarged scutes, the posteriormost subconical, pointing backward, largest median one having a basal width of 23 mm and projecting 31 mm; the 2 scutes touching its sides somewhat smaller. Jaw slightly hooked but this not very obvious. Tail somewhat flattened at base with 8 or 10 pairs of supracaudal scales, and terminating in a grooved, spurlike tubercle.

Color in life: Above, carapace a shade of olive-black; vertebral and costal shields each with a rather large horn-colored area covering the central part; marginals, including nuchal and supracaudals each with a horn-colored mark on its central outer part; plastron largely yellowish with blackish areas, flecks or clouding; large scutes covering outer surface of arms and legs of varying shades of horn color often edged with a darker color or sometimes entire scale olive; skin on exposed surfaces of neck and limbs a dirty indefinite yellowish olive.

Measurements in mm:* Length of carapace, 455, 434; width of carapace, 315, 295; length of plastron, 463, 448; length of suture between gulars, 70, 72; suture between humerals, 88, 63; between abdominals, 173, 165; between femorals, 45, 50; between anals, 43, 33; length and width of vertebrals, first, 104-87, 118-88; second, 129-83, 110-75; third, 135-100, 110-86; width of nuchal,

* Measurements taken from the described form and another living specimen in the Bangkok Zoo (Dusit), respectively. I have not obtained accurate measurement of the head and legs of the latter.

28-22, length of nuchal, 31, 26; width and length of costals, first, 103-100, 120-108; second, 87-124, 96-130; third, 81-116, 86-119; fourth, 86-79, 93-82; tail, 52, 48.

Variation: The costal shields in the adult are not always concave. Sometimes the plastron is actually longer than the carapace. While the pectoral shields are usually separated, they rarely touch. The inguinal is sometimes single.

Some specimens are much darker than others; the second measured specimen is considerably darker than the one described. The horn-colored spots can be seen but they are very inconspicuous.

Remarks: These large turtles are now becoming rare in Thailand. They are seldom found except in more or less uninhabited hilly or mountainous districts. They are generally utilized as food throughout Thailand.

These turtles are herbivorous, and are said to be fond of water, which is not true of many species of the family Testudinidae. Some American desert forms are capable of going for weeks without water other than that which they manufacture in metabolism.

Testudo emys is the largest Asiatic species of the genus and it may readily be distinguished from other Thai species, *elongata* and *impressa,* by the separation of the pectoral shields from one another on the plastron. The division of the subcaudals, however, occurs also in *impressa* but not in *elongata.*

Both in Thailand and in Malaya the species is known as the six-footed-turtle because of the greatly enlarged conical scutes on the back of the thigh which simulate the rough scutes of a retracted foot. Boulenger (1912) states the Malay name is *kura kura anam kaki.*

Distribution: The species has been reported in Thailand from the province of Nakhon Si Thammarat but probably occurs in the mountain areas throughout the peninsular parts.

Outside of Thailand the species ranges in Burma, Assam, Malaya, Sumatra, and some smaller islands of the Indo-Australian Archipelago. M. Smith (1931a) questions the reports of Tirant (1885a) for Saigon: of Mell (1922a) for Canton, and of Siebenrock (1909) for the mouth of the Yang Tse Kiang.

This species is figured by Dr. Boonsong Lekagul (1966, pp. 57-58).

Testudo impressa (Günther)

(Fig. 8)

Geoemyda impressa Günther, Proc. Zool. Soc. London, 1882, p. 343, figs. 1-3 (type-locality, Siam).

Testudo impressa, M. Smith, Jour. Nat. Hist. Soc. Siam, vol. 4, no. 4, July 25, 1922, pp. 204-205; The fauna of British India including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 145-146; Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5. 1955, p. 379.

Testudo emys Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the

British Museum, 1889, p. 158 *(part.)*; The fauna of British India, . . . Reptilia and Batrachia, 1890, p. 22 *(part.)*; Ann. Mus. Civ. Genova, 1893, ser. 2, vol. 13, p. 312.

Geoemyda latinuchalis Valliant, Bull. Soc. Philom. Parsi, 1894, ser. 8, vol. 6, p. 68 (type-locality, Rivière Noire, Tonkin); Mocquard, Rev. Colon. Rept. Indo-Chine, 1907, p. 10.

Testudo latinuchalis, Siebenrock, Zool. Jahrb., Suppl., 1909, vol. 10, p. 520; Boulenger, A vertebrate fauna of the Malay Peninsula. . . . Reptilia and Batrachia, 1912, pp. 15-16.

Testudo pseudemys Boulenger, Fasciculi Malayenses, Zoology, 1903, vol. 1, p. 144, pl. 9, text fig. 1, skull (type-locality, Batang Padang district, Perak); Annandale, Jour. Proc. Asiat. Soc. Bengal, 1906, ser. 2, vol. 2, p. 204.

Diagnosis: Land tortoise reaching a carapace length of 270 mm. Carapace much flattened on dorsal surface, vertebral and costal scutes somewhat concave, the marginals somewhat recurved laterally and posteriorly; vertebrals as wide or nearly as wide as costals; upper and lower part of arms covered with large imbricating scales, those on front surface of arm spinelike, tips elevated; top of head with symmetrical shields.

Description of species (from a dried shell, No. 1647): Carapace strongly serrated all around its margin, dorsal surface strongly flattened, vertebral and costal plates somewhat concave; some marginals distinctly recurved or flaring; nuchal scute distinctly wider than long (22 x 12 mm), anterior part with two spinelike denticulations distinctly shorter than adjoining marginals (28.5 mm); measurements of vertebrals, width x length in mm: first, 43 x 35, sides parallel for much of its length; second, 55 x 27.5; third, 56 x 28, ends parallel; fourth, 52 x 34; fifth, 47x 34. Measurements of costals, length x width in mm: first, 37 x 48; second, 36 x 54; third, 37 x 52; fourth, 35 x 35; subcaudals divided with a A-shaped notch.

Plastron wide, with a distinct bridge, broadly notched anteriorly and posteriorly, shorter than carapace; gulars with small spinelike processes; pectorals with a notch near axillary scute; inguinal and axillary scutes well developed, former divided in two on one side; length of median sutures in mm: gular, 15; humeral, 36; pectoral, 10; abdominal, 52; femoral or inguinal, 24; anal, 17. Length of bridge considerably longer than posterior lobe; areolar area of abdominals slightly elevated. Lines of growth on plastron and carapace strongly marked and alveolar areas of carapace clearly corrugated, borders of the scutes sharply angular. Posteriorly plastron and carapace almost touch.

Arms somewhat flattened, fingers scarcely separated, without web; front face of upper and entire lower arm with heavy, enlarged, bony, imbricating scutes, some sharply pointed and with points elevated; leg similarly scaled, largest scales spinelike; scales on heel; foot hooflike, sole covered with large, slightly imbricating scales; tail short with paired scales below, upper part covered with irregular scales; a very large conical scute on thigh, 12 mm high.

Head moderately large, top with more or less symmetrical shields consisting of a frontal preceded by 2 pairs of shields; upper jaw not or but slightly hooked. Some small dark spotted scales back of jaws.

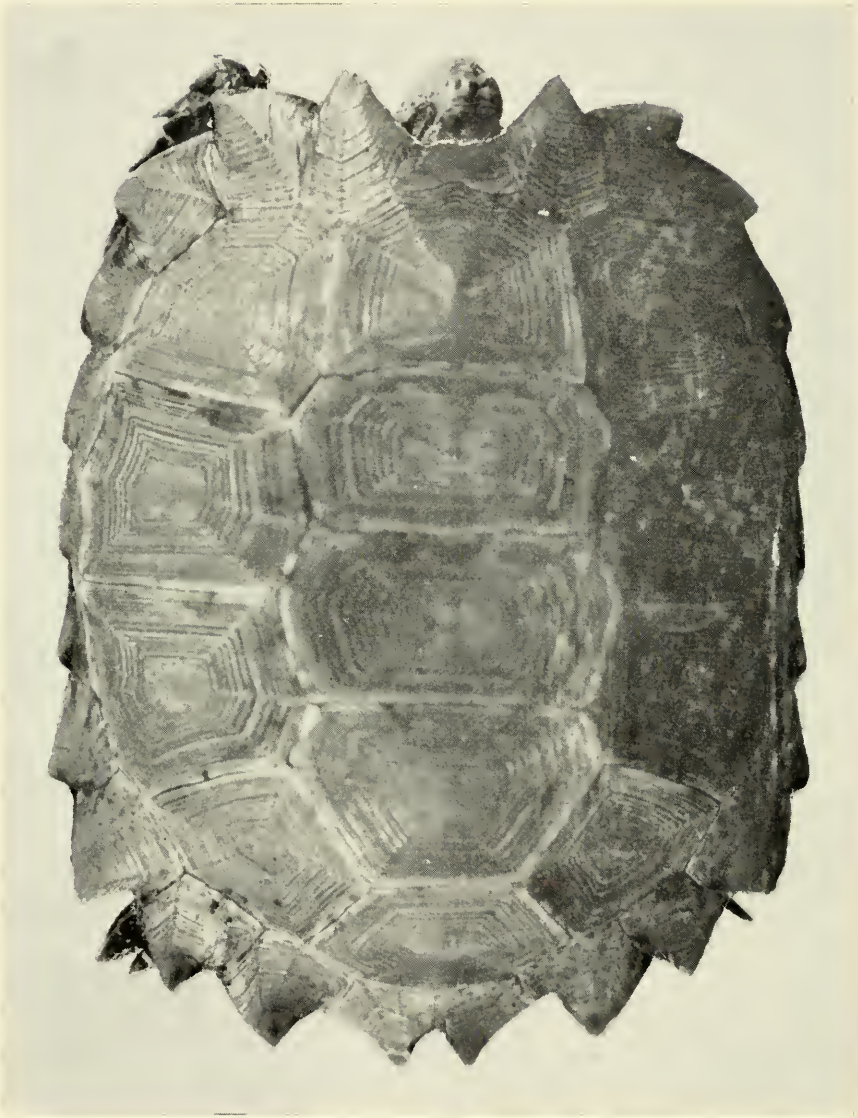

FIGURE 8. *Testudo impressa* (Günther). Chulalongkorn Univ. No. 1647, Carapace length, 166 mm; carapace width, 140 mm.

Color: Light brown of varying shades, lighter near sutures; about periphery of each scale, short dark brown radiating lines. Laterally on marginals some indefinite larger dark spots; plastron yellow-brown becoming pale yellowish near sutures; distal remnants of radiating lines.

Arms nearly black; legs and tail very dark brown.

Measurements in mm: Length of carapace, 166; width of carapace, 140; depth of shell, 73; length of plastron, 161; width of plastron, and bridge (pectorals), 123; width of anterior lobe, 96; width of posterior lobe, 91; length of posterior lobe, 56; length of bridge, 68.

Variation: The described specimen is considerably more than half grown as the species reaches a length of at least 270 mm in carapace length.

Young specimens may be light yellowish brown above, finely speckled with black. Some specimens have strongly defined dark rays on the plastron.

Distribution: In Thailand the species has been taken in relatively few places. It is a mountain species found at moderate altitude. The type was taken in Thailand but the exact locality is unknown.

Malcolm Smith (1916c) reports a series of specimens taken in Thailand but does not give exact localities. It is not a common species. The specimen here described has no specific locality recorded.

Remarks: The sculpturing of the carapace, the strongly serrate character of the marginals, and the rich brown coloration of the carapace combine to make this perhaps the handsomest of the turtles and tortoises of Thailand.

Several excellent figures of this species are given by Dr. Boonsong Lekagul (1966, p. 59).

Superfamily **Chelonioidea**

Head partially retractile, forming an S-shaped curve in a vertical plane; cervical vertebrae short; outer part of the tympanic cavity not roofed over by bone.

Pterygoid bones forming a median suture anteriorly, posteriorly rather widely separated; squamosals and parietals forming a suture. A complete set of marginal bones joined to the ribs. Pelvic girdle not fused to carapace or plastron. Carapace bones covered with horny epidermal shields.

One family, the Cheloniidae, is associated with this superfamily.

Family **Cheloniidae** Gray

Nuchal plate lacking a riblike process. Nine plastral bones. Temporal region of skull roofed over completely. Plastral elements reduced in size with a median vacuity between the 2 lateral halves, and connected to carapace by ligamentous tissues. Costal plates above ribs covering most of dorsal area in one form *(Chelonia),* leaving wide fontanelles between them and marginal bones. In *Eretmochelys* they may reach the marginals in old age. In others the fontanelles may disappear in adult.

The family Cheloniidae Gray consists of four recognized genera each comprising a single species: *Caretta* Rafinesque, *Chelonia* Latreille, *Eretmochelys* Fitzinger and *Lepidochelys* Fitzinger. These may be separated by the following key:

KEY TO GENERA OF THE CHELONIIDAE

1. Five or more pairs of costal shields 3
   Four pairs of costal shields 2
2. Two pairs of prefrontal shields; dorsal scutes on carapace imbricate, tending to become juxtaposed in very old specimens; jaws hooked ..... *Eretmochelys*
   One pair of prefrontal shields on head; dorsal scutes on carapace always juxtaposed; jaws not hooked ..... *Chelonia*
3. Normally 6 pairs of costals; interegular shield usually present (sometimes divided); usually 27 marginals; carapace reaches a length of 1050 mm ..... *Lepidochelys*
   Normally 5 pairs of costals. Three relatively large inframarginal scutes. Last few neural plates may be separated by costal plates which meet on midline. Color usually dull reddish brown; 2 pairs of prefrontals, marginals usually less than 27 ..... *Caretta*

Genus **Eretmochelys** Fitzinger

Eretmochelys Fitzinger, Systema Reptilium, 1843, p. 30 (type of genus, *imbricata*).

Diagnosis: Four pairs of costal shields; an intergular shield; a series of inframarginal shields between carapace and plastron; 3 or 4 axillaries and 1 or 2 inguinal shields; regular plastral scales keeled, anals with highest keels. Head covered with regular shields consisting of a frontal preceded by 2 pairs of scales, a pair of supraorbitals, parietals, occipitals, 2 large supratemporals, and 8 or 9 temporals; arms flipperlike; legs similar, shorter, widened; carapace covered with strongly imbricating shields, all keeled with accessory nonparallel ridges; a nuchal, 5 ventral, 4 costal, and 24 marginal shields; jaw hooked; a large shield following the shield on lower jaw; usually 2 claws on hand and foot.

Only a single species with two subspecies is recognized. These may be distinguished by the following key:

KEY TO SUBSPECIES OF *Eretmochelys imbricata*

1. Carapace somewhat straight-sided and narrowly tapered behind; upper surface of head and flippers with less black coloration. Atlantic Ocean, Caribbean Sea ..... *imbricata imbricata*
   Carapace usually somewhat heart-shaped in lateral outline, upper surface of head and flippers almost solid black. Indian and Pacific Oceans ..... *imbricata bissa*

Eretmochelys imbricata bissa (Rüppell)

(Figs. 9-10)

Caretta bissa Rüppell, Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, 1835, p. 4 (type-locality, Red Sea).

Eretmochelys squamata Agassiz, Contribution to the natural history of the United States of

America, vol. 1, 1857, p. 382 (type-locality, restricted to Singapore); M. Smith, The fauna of British India. . . . Reptilia and Amphibia, vol. 1, Loricata, Testudines, Mar. 1931, pp. 67-69, fig. 12.

Chelone imbricata Boulenger, Catalogue of chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 183; The fauna of British India, including Ceylon and Burma, Reptilia and Batrachia, 1890, p. 49.

Chelonia imbricata Siebenrock, Zool. Jahrb. Jena (Suppl.) 10, Heft 3, 1909, p. 547 *(part.)*.

Caretta squamata, Günther, The reptiles of British India, 1864, p. 54.

Eretmochelys imbricata, Taylor, Amphibians and Turtles of the Philippine Islands, 1921, pp. 180-182, pl. 15, figs. 1, 2; pl. 16, figs. 5, 6.

Caretta rostrata Girard, U.S. Exploring Expedition, Herpetology, 1858, p. 442, pl. 30 (type-locality, Fiji Islands).

Eretmochelys imbricata bissa, Smith and Taylor, Bull. U.S. Nat. Mus. Washington, no. 199, 1950, p. 16; Mertens und Wermuth, Die rezenten Schildkröten. . . . Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 385.

Diagnosis: Characters of genus.

Description of species (from No. 1652, Gulf of Siam): Carapace low, covered with strongly imbricating shields; a well-defined sharp median keel; lateral keels dim, indistinct; nuchal wide, nearly double width of adjoining marginals; more than twice as wide as long (from nuchal edge); all vertebrals distinctly wider than long (from overlapping edge of preceding scale); first 3 costals distinctly larger than vertebrals; all costals wider than long. Vertebrals and to lesser extent costals with 2 accessory keels lateral to median, which tend to converge posteriorly on each scale; carapace serrate, lateral and posterior marginals terminating in a sharp, rather spinelike projection; supracaudals with a slight posterior notch.

Carapace rather flattened on a level with border of carapace; a triangular median intergular; measurements in mm of the plastral sutures are: gulars, 21; humerals, 30; pectorals, 32; abdominals, 37; femorals, 37; anals, 46. Plastral shields with continuous keels converging somewhat at each end of carapace, highest posteriorly; a row of 4 flat intercalated shields between plastron and carapace, all a little longer than wide; 5 smaller axillary shields and 2 small inguinal scales, the latter separated.

Arms paddle-shaped, with 2 claws evident on distal anterior edge of paddle; front face of paddle covered with enlarged scutes arranged in several irregular rows; underside (posterior) face with similarly enlarged scutes more irregularly arranged; front face of leg and foot with irregular rows of scutes; posterior face with numerous enlarged, as well as small scutes.

Tail very short, dorsal part with 2 or 3 paired scales; a specialized shield follows postanals.

Head covered with shields (or scutes), consisting of a large shield covering most of upper jaw and beak, small soft plate through which both nostrils are pierced, a pair of supranasals, a larger pair of prefrontals preceding a single frontal flanked by large supraorbitals, a pair of fused parietals, and a pair of occipitals. Eight temporals follow supraorbital; an elongate scute follows the large scute on lower jaw.

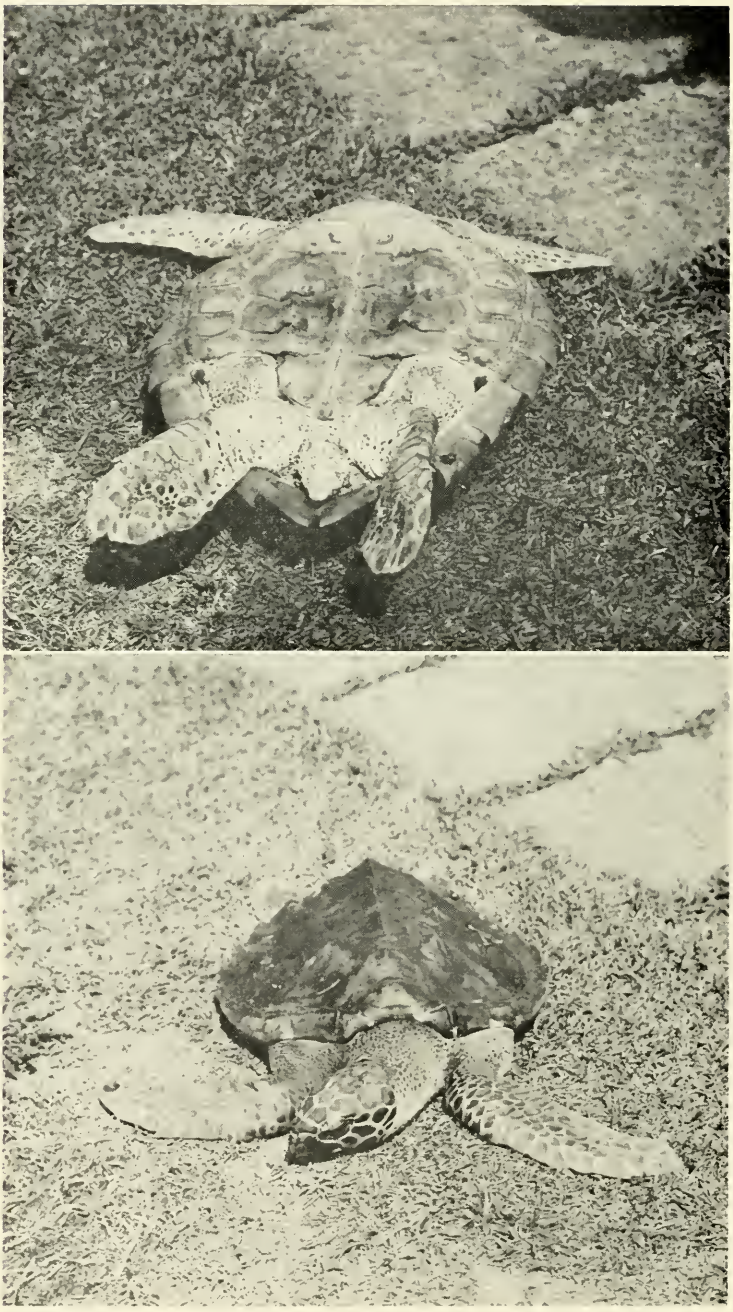

FIGURE 9. *Eretmochelys imbricata bissa* (Rüppell). Philippine Bureau of Science No. 1474. Carapace length, 173 mm. Upper figure, ventral view; lower, dorsal view.

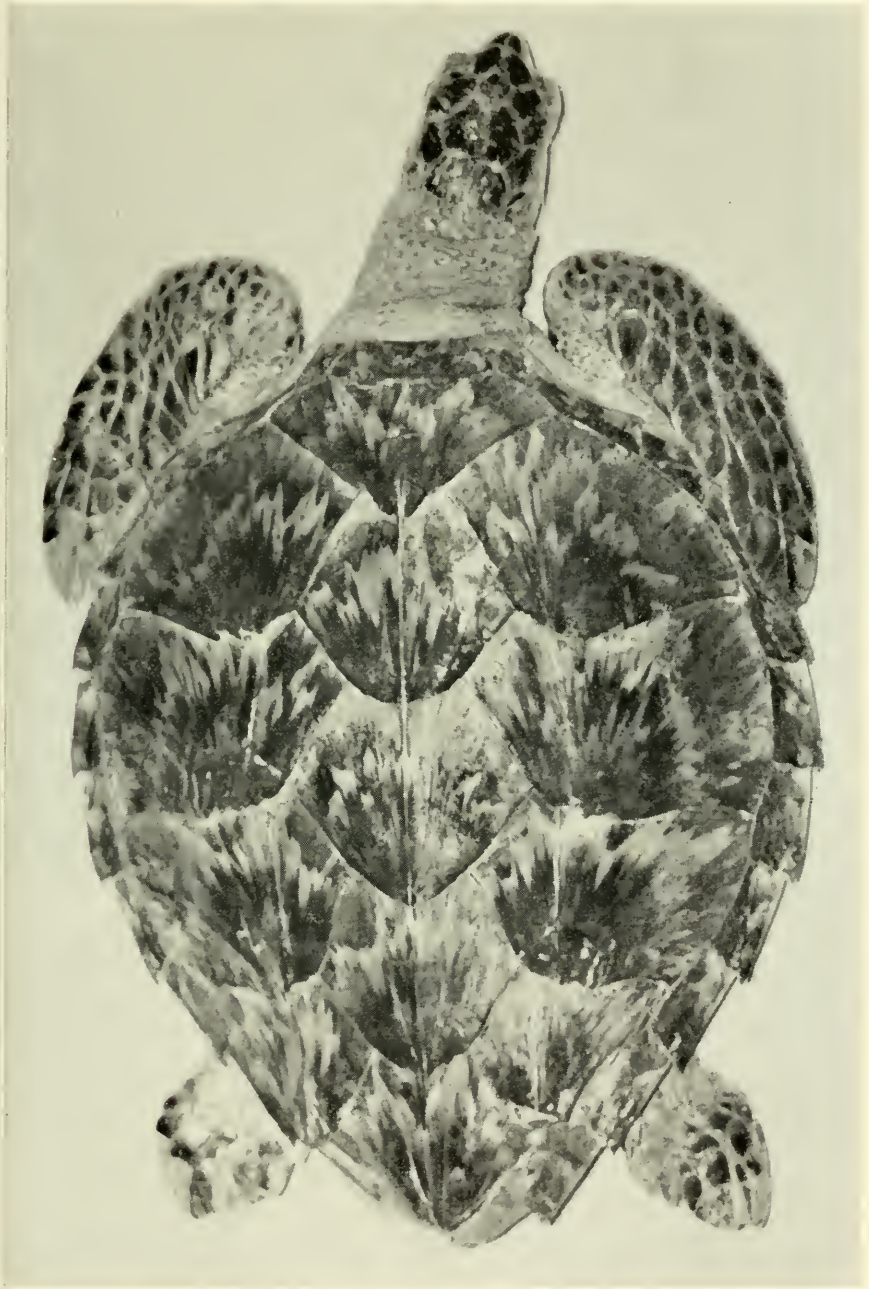

Figure 10. *Eretmochelys imbricata bissa* (Rüppell). Philippine Bureau of Science No. 1474 (young). Aparri, Luzon. Carapace length, 245 mm.

Color: Above brown, streaked with amber; plastron light yellowish, darker along posterior part of keels; scales of head, arms, and legs brown, often with yellowish borders.

Measurements in mm: Total length, 244; length of carapace, 173; width of carapace, 130; length of plastron, 134; width of plastron across pectorals, 81; length of arm, 98; length of leg, 53; head length, 47; head width, 30 (from Taylor [1921], Philippine specimen, No. 1474 Bureau of Science Coll.; Manila).

Variation: The dorsal shields, normally imbricate, may become practically juxtaposed in very old animals.

Distribution: In Thai waters the species occurs around the entire coast-line but nowhere is it regarded as common as other species of marine turtles.

It is widely distributed along tropical and subtropical coast-lines of the Pacific and Indian Oceans.

Remarks: This species furnishes the "turtle shell" of commerce. It is still collected, but now has to compete with artificial "tortoise shell."

Genus **Chelonia** Brongniart

Chelonia Brongniart, Bull. Sci. Soc. Philom., vol. 2, 1800, p. 89 (type of genus, *Chelonia mydas*).

Diagnosis: Five vertebrals, 4 pairs of costal shields. An intergular scale separating anterior part of gulars. A series of inframarginal scales (4 or 5). Eleven pairs of marginals and 1 pair of supracaudals. Head with regular symmetrical scales. One pair of prefrontals; nuchal transversely widened. Jaws not hooked.

A single species is recognized with at least two subspecies. They occur in the Atlantic, Pacific, and Indian Oceans.

Chelonia mydas Linnaeus

Testudo mydas Linnaeus, Systema Naturae, ed. 10, vol. 1, p. 197 (type-locality [restricted by Mertens and Müller, 1928], Asuncion Island).

Chelonia mydas japonica (Thunberg)

(Fig. 11)

Testudo japonica Thunberg, Kongl. Vetensk. Acad. Handl., Stockholm, 1787, vol. 8, p. 178 (type-locality, Japan).

Caretta thunbergii, Merrem, Tentamen Systematis Amphibiorum, 1820 (substitute name for *T. japonica* Thunberg).

Chelonia mydas japonica, Gray, Synopsis Reptilium or short descriptions of the species of reptiles, pt. 1, Cataphracta, tortoises, crocodiles and enaliosaurians, pt. 1, p. 53; Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, pp. 384, 385.

Chelonia formosa Girard, U.S. Exploring Expedition, Herpetology, 1858, p. 456 (type-locality, Fiji Islands).

Chelonia tenuis Girard, U.S. Exploring Expedition, Herpetology, 1858, p. 459 (type-locality, "Tahiti, Honden, Eimeo and Rosa Islands").

Chelonia agassizii Bocourt, Ann. Sci. Nat., Paris, ser. 5, vol. 10, 1868, p. 122 (type-locality, mouth of Río Nagualate, Pacific Coast of Guatemala).

Chelonia lata Philippi, Zool. Garten, Frankfurt am Main, 1887, vol. 28, p. 84 (type-locality, Valparaiso, Chile).

Chelonia japonica Taylor, Amphibians and Turtles of the Philippine Islands, Manila, Pub. 15, Bureau of Science, 1921, pp. 184-185, pl. 17, figs. 1-4.

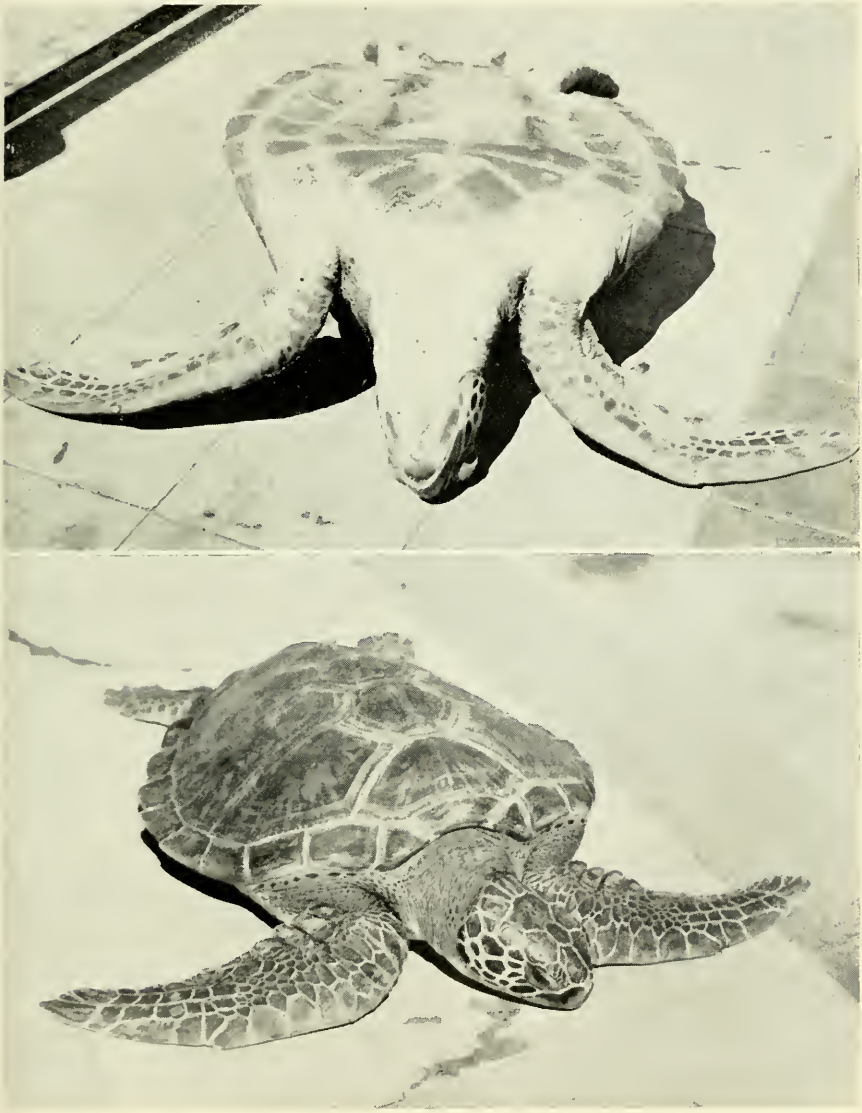

FIGURE 11. *Chelonia mydas japonica* Thunberg. Specimen living in the Manila Aquarium. Manila Bay, near Manila. Carapace length, 735 mm. (Also figured in Taylor, 1920.) Upper, ventral; lower, dorsal view.

Diagnosis: Limbs paddle-shaped, with 1 or 2 claws. Shell covered with horny shields; costal plates fused to ribs and carapace, not extending to edge of carapace. Having other characters of the genus.

Description of species: Large marine form commonly known as the Green Turtle. Carapace longer than wide, somewhat arched, slightly serrate posteriorly; 11 pairs of marginals, a broad nuchal and paired supracaudals border rim of carapace; 5 vertebrals wider than long; 4 pairs of costals. Plastron separated from marginals by a series of 4-5 inframarginals; 6 pairs of plastral shields with a single intergular preceding the gular pair.

Head rather large, the snout short; edges of the jaws denticulated, much more strongly so on the lower jaw; upper alveolar surface of upper jaw with 2 strongly denticulated ridges; lower jaw with a short symphysis. One pair of prefrontal shields. Limbs paddle-shaped usually with only a single claw present.

The young specimens usually with a median keel, sometimes with a lateral keel also. Young may have 2 claws. Their color olive to dark brown with some yellow markings on limbs; venter yellowish, with dark areas on hands and feet. The adults are likewise greenish to grayish brown. Some specimens show dark rays. Plastron yellow.

The length of the shell often exceeds a meter.

Measurements in mm: Total length, 735 (head to tail); length of carapace, 555; width of carapace, 470; height of shell, 180; length of plastron, 448; width of plastron across pectorals, 125; width of head, 90; depth of head, 100; tail, from vent, 28.

Remarks: Despite the paddle-shaped limbs the original bony system of limbs and girdle is present with only a few exceptions. The fontanelles between the marginals and costals are never completely covered by bone in this genus.

This species is widely eaten. Sir J. E. Tennant (1861), former civil secretary to the colonial government of Ceylon, reports a case of a turtle of this species being eaten in Ceylon causing the death of 18 persons. This was October 1840.

Taylor (1922) reports a similar case from Cebu Island where a turtle was consumed by 33 persons, 14 of whom died. It is not known whether the meat becomes poisonous only at certain seasons, or age, or whether it is due to some type of poisonous plant consumed by the turtle or by some disease. It is not impossible that the meat had been allowed to spoil before being consumed but there was no evidence that this was true in the latter case.

Genus **Lepidochelys** Fitzinger

Lepidochelys Fitzinger, Systema Reptilium, 1843, p. 30 (type of genus, *Lepidochelys olivaceus* (Eschscholtz)); Carr, Proc. New England Zool. Club, vol. 21, 1942, p. 4.
Chelonia Eschscholtz, Zool. Atlas, 1, 1829, p. 3.

Diagnosis: "Maxillaries not in contact, separated by vomer; frontal bone entering rim of orbit; pterygoids markedly broadened anteriorly, the ectopterygoid process strong; fontanelles in choanal chamber near opening, not hidden by alveolar surface in ventral aspect; external opening of orbits not concealed by overlying bones in ventral aspect; descending processes of prefrontals not reaching palatines; lower jaw with a more or less sharp and strong triangular median element at the posterior border of the bony alveolar surface, which may or may not extend forward as an elevated ridge; four enlarged inframarginal scutes on the bridge; neural bones 11-15; color gray to olive green." (Carr, 1942.)

Lepidochelys olivacea (Eschscholtz)

Chelonia olivacea Eschscholtz, Zool. Atlas, 1, 1829, p. 3, pl. 3 (type-locality, Manila Bay, Philippines).

Three subspecies of *olivacea* are recognized by the Mertens-Wermuth List (1955). These are the typical *L. o. olivacea, L. o. kempi* (Garman) and *L. o. remivaga* (Hay). These 3 may be contrasted by the following brief diagnoses:

L. o. olivacea: Bony alveolar surface of each side of upper jaw usually with a gentle elevation extending parallel to the cutting edge but never with a conspicuous ridge; combined width of pterygoids behind expanded anterior portion usually contained no more than 2-2.5 times in greatest diameter of orbit; each inframarginal scute usually with a pore at its posterior border; costal scutes usually in more than 5 pairs; color olive. Indian and Pacific Oceans.

L. o. kempi: Bony alveolar surface of upper jaw with a median ridge extending parallel to the cutting edge; combined width of pterygoids, behind expanded anterior portion, contained about 3 times in greatest diameter of orbit; inframarginal scutes without pores; costal scutes usually in 5 pairs; color usually gray. Atlantic Ocean, Gulf of Mexico.

L. o. remivaga: Described by Hay (1908) from a skull from Ventosa Bay, Gulf of Tehuantepec, Mexico (without a carapace) chiefly by a comparison with that of *Caretta*. "The skull is flat, the snout more or less pointed. The frontal bones enter the rim of the orbit; maxillae are widely separated by the vomer. The pterygoids possess conspicuous ectopterygoid processes. The free border of pterygoid when followed backward becomes a ridge which disappears before it reaches the pedicel of the quadrate. Occipital condyle stands distinctly behind the quadrates. Prootic bones project but little in front of the pedicels. The frontal scute is about as long as the frontoparietal; the latter is not so long as the parietals. Known from Ventosa Bay, Gulf of Tehuantepec, Eastern Pacific Ocean."

Lepidochelys olivacea olivacea (Eschscholtz)

(Fig. 12)

Chelonia olivacea Eschscholtz, Zool. Atlas, 1829, vol. 1, pl. 3 (type-locality, Manila Bay, Philippines).

Caouana olivacea, Gray, Catalogue of the tortoises, crocodiles and amphisbaenians in the collection of the British Museum, 1844, p. 53; Günther, Reptiles of British India, p. 52.

Caretta olivacea, Garman, Bull. Mus. Comp. Zool. Harvard College, vol. 52, 1908, p. 9; Taylor, Amphibians and turtles of the Philippine Isands, Dept. Agri. Nat. Resources, Bureau of Science, Manila, No. 15, Dec. 15, 1921, pp. 182-184, pl. 17, figs. 1-4.

Thalassochelys olivacea, Boettger, Ber. Senck. Nat. Ges., 1886, p. 93.

Chelonia dussumierii Duméril and Bibron, Erpétologie Générale, vol. 2, 1835, p. 557.

Lepidochelys olivacea, Girard, U.S. Exploring Expedition, Herpetology, 1858, p. 435; Mertens and Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 386.

Caretta caretta olivacea, M. Smith, The fauna of British India . . . including Ceylon and Burma. Reptilia and Amphibia, vol. 1, 1931, pp. 71, 72.

Diagnosis: Characters of the genus. Normally, 6 pairs of costals; intergular shield usually present, sometimes divided; usually 27 marginals. Carapace reaches a length of 1050 mm or more.

Description of species: Carapace with a distinct median keel, more prominent posteriorly; 6 pairs of costals, the nuchal divided; 6 vertebrals, the fifth small; 11 pairs of marginals with 2 supracaudals and 2 nuchals; a small inguinal shield, and a group of small axillary shields, 4 of which touch pectorals and humerals. A small round shield behind the anal shields.

The head scales on a Philippine specimen examined consisted of a pair of anterior prefrontals smaller than the second pair; an azygous prefrontal between 2 supraoculars; frontal large, wider than long, followed by 4 parietals; a large temporal (parietal) follows the supraocular and borders the frontal and parietal; 3 postoculars, upper smallest, middle largest, lower elongate; postoculars bordered by 4 temporals.

Color: Drab olive or gray-olive, somewhat lighter at sutures. Sides and underside of neck whitish. Plastron whitish with somewhat darker areas on plastral scutes.

Measurements in mm (Young living specimen): Length of carapace, 340; width of carapace, 325; height of carapace, 110; length of arm, 260; length of leg, 180; length of plastron, 275; width of plastron, 280; tail from vent, 15; length of head to end of parietals, 90; depth of head, 55.

Remarks: The subspecies is widely distributed in the Pacific and Indian Oceans. The young show indistinct dorsal and ventral keels.

Genus **Caretta** Rafinesque

Caretta Rafinesque, Specchio Sci. Palermo, vol. 2, 1814, p. 66 (type of genus, *Caretta nasuta* Rafinesque=*Testudo caretta* (Linnaeus)).

Diagnosis: "Five or more pairs of costal shields; intergular shield present or absent. A series of inframarginal plastral shields. Head covered with symmetrical shields; two pairs of prefrontals. Tail short." M. Smith (1931a).

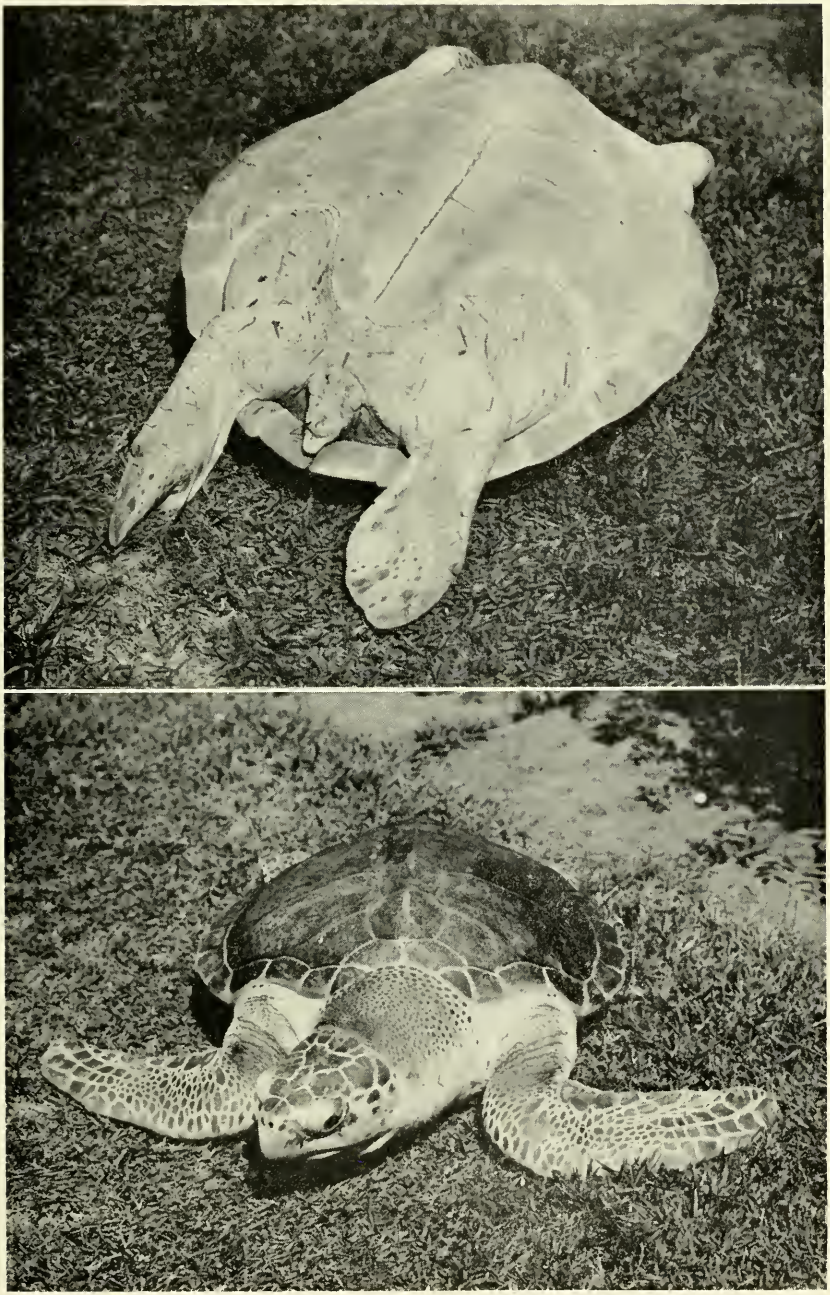

Figure 12. *Lepidochelys olivacea olivacea* (Eschscholtz). Specimen living in Manila Aquarium. Topotype, Manila Bay. Carapace length, 340 mm. Upper, ventral; lower, dorsal view.

There is considerable variation in the number of the shields that compose the carapace. The amount of variation is in part geographical as the greatest variation occurs in the Indian and Pacific Oceans.

Caretta caretta (Linnaeus)

Testudo caretta Linnaeus, Systema Naturae, ed. 10, 1758, vol. 1, p. 197 (type-locality restricted to Bermuda).

This species is regarded as comprising two subspecies, *Caretta c. caretta* Linnaeus and *C. c. gigas* Deraniyagala.

KEY TO SUBSPECIES OF *Caretta caretta*

1. Marginal scales on each side averaging 12; neural bones usually 7 or 8, rarely interrupted by costal plates (pleurals). Atlantic Ocean, Mediterranean Sea ..... *caretta caretta*

   Marginal scales usually 13 on each side; neural bones 7-12, the last bones of series (1-5) usually interrupted by costal plates (pleurals), which are in contact with each other. Indian and Pacific Oceans ..... *caretta gigas*

Caretta caretta gigas Deraniyagala

Caretta gigas Deraniyagala, Ceylon Jour. Sci., sec. B, vol. 18, 1933, p. 66 (type-locality, Gulf of Mannar, Ceylon).

Caretta caretta gigas, Deraniyagala, Tetrapod reptiles of Ceylon, vol. 1, 1939, p. 164.

Caretta caretta gigas, Mertens and Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 383.

Caretta caretta olivacea, M. A. Smith, The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, Mar. 1931, pp. 71-72 *(part.)*.

Diagnosis: Differs usually but not invariably from the typical form in having 3 relatively large inframarginal scutes; usually 5 pairs of costals. The last few neurals interrupted by pairs of costals forming a median suture. The color, varying shades of reddish brown.

Description of subspecies: Characters of the genus.

Nuchal scute single; normally 5 costals. Marginals somewhat variable, 11-13 pairs. Plastron with paired gulars, pectorals, abdominals, femorals and anals, the lengths of sutures not differing greatly. Head with 2 pairs of prefrontals; frontoparietal large; 2 or 3 pairs of parietals; 2 supraoculars on each side; other postoculars and temporal scales somewhat variable.

Arms in the form of elongate paddles, each bearing 2 claws (rarely 1). Legs large but shorter than arms, the width and length nearly equal. Both arms and legs with scales and scutes of variable size, largest on inner edge of arm around posterior parts of each.

Carapace somewhat arched, longer than wide, and with posterior parts narrowed. Young with 3 keels above and 4 on the plastron below.

Remarks: Most of these data are from Deraniyagala, who gives a very detailed description of the typical form. The subspecies is widely distributed from Australia to Ceylon along the coast of southeast Asia and the islands of the Pacific Ocean.

I believe that this subspecies is exceeded in size only by *Dermochelys coriacea*.

Superfamily **Trionychoidea** Fitzinger

Head capable of being withdrawn completely within shell, neck forming a sigmoid curve in a vertical plane. Bones of carapace and plastron covered with soft skin instead of horny plates. Phalanges not free, encased in a paddlelike limb; arm with 2 or 3 claws. Pterygoids not forming a suture; basisphenoids forming sutures with palatines. Only a single Asiatic family, the Trionychidae, is associated with this superfamily.

Family **Trionychidae** Bell

Trionychidae Bell, Zool. Jour., vol. 3, 1828, p. 515.

Genus **Trionyx** Schweigger

Trionyx Schweigger, in Geoffroy Saint-Hilaire, Ann. Mus. Nat., Paris, vol. 14, 1809, p. 1 (type of genus *Testudo cartilaginea* Boddaert).

The differences between *Amyda* and *Trionyx* would seem to be not easily discerned. Both names appear in the same publication (Schweigger, *vide* supra), the type of *Trionyx* being *Trionyx coromandelicus* Geoffroy Saint-Hilaire (*Trionyx punctatus granosus* Schoepff). Various herpetologists have used the name *Trionyx* for this group of soft-shelled turtles; others have used *Amyda* which has page priority.

In certain recent publications authors have retained *Trionyx* for the greater number of the soft-shelled turtles of America, Africa and Asia. The group designated *Trionyx* by Geoffroy Saint-Hilaire were the "three toed" turtles with 7 plastral callosities. Malcolm Smith (1931a) regarded this group as equivalent to *Emyda* Rafinesque but shows that this name as used by Gray is a homonym of that of Rafinesque which was proposed as a substitute name for *Emys* Duméril. Smith then proposes a new name—*Lissemys*—for the group having 3 toes and 7 plastral callosities and a "cutaneous femoral valve" with marginal bones.

Diagnosis: Thus *Trionyx* may be defined as lacking a cutaneous valve, marginal bones, and as having 4 plastral callosities. Orbit nearer to temporal cavity than to nasal cavity; arch following orbit narrower than orbital diameter; proboscis as long as eye opening. The dorsal surface of the young bears longitudinal series of small tubercles.

Trionyx cartilaginea (Boddaert)

Testudo cartilaginea Boddaert, Epistola ad W. Roell, cum tab. 1770, pp. 1-39 (type-locality unknown).

Trionyx cartilagineus, Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 253, fig.; The fauna of British India. . . . Reptilia and Batrachia. 1890, p. 15; Siebenrock, Sitzungsb. Akad. Wiss. Wien, vol. 112, pt. 1, 1903, p. 347; Zool. Jahrb. Jena, Suppl. 10. Heft 3, 1909, p. 599; de Rooij, The reptiles of the Indo-Australian Archipelago, vol. 1, Lacertilia, Chelonia, Emydosauria, 1915, pp. 329-330, fig. 127; Annandale, Rec. Ind. Mus., vol. 7, pt. 2, 1912, p. 168; M. Smith, The fauna of British India, . . . including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata and Testudines, Mar. 1931, pp. 174-175, figs. 31-33.

Testudo rostrata Thunberg, Kongl. Vet.-Akad. N. Handl., Stockholm, vol. 8, 1787, p. 179, pl. 7 (type-locality, India).

Trionyx stellatus Geoffroy-Saint Hilaire, Ann. Mus. Nat. Hist. Paris, vol. 15, 1809, p. 13 (type-locality?); Theobald, Proc. Asiat. Soc. Bengal, 1874, p. 79, pl. 3; *ibid.,* 1875, p. 176, pl. 5.

Trionyx Javanicus Geoffroy Saint-Hilaire, Ann. Mus. Nat. Hist., Paris, vol. 15, 1809, p. 15, pl. 3 (type-locality, Java).

Trionyx caviniferus Gray, Catalogue of the shield reptiles in the collection of the British Museum, part 1, Testudinata (Tortoises), 1855, p. 67, pl. 32 (type-locality, Moluccas); Theobald, Proc. Asiat. Soc. Bengal, 1874, p. 80, pl. 4.

Trionyx ornatus Gray, Proc. Zool. Soc. London, 1861, p. 41, pl. 5 (type-locality, Cambodia).

Aspilus punctulatus Gray, Proc. Zool. Soc. London, 1864, p. 84 (type-locality, Amboyna or Ceram).

Trionyx jeudi Gray, Proc. Zool. Soc. London, 1869, p. 217, fig. (type-locality, ? Dutch East Indies).

Trionyx ephippium Theobald, Proc. Asiat. Soc. Bengal, 1875, p. 177, pl. 5 (type-locality, Tenasserim).

Amyda cartilaginea, Barbour, Mem. Mus. Comp. Zool. Harvard Coll., vol. 44, 1912, p. 144; Mertens and Wermuth, Zool. Jahrb. (Syst.), 1955, Band 83, Heft 5, p. 387.

Trionyx phayrei Theobald, Jour. Linn. Soc., London (Zool.), vol. 10, 1870, p. 18 (type-locality, Mts. of Arakan, Bassein District, West Pegu, Burma); Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the collections of the British Museum, 1889, p. 251.

Diagnosis: A single neural plate between anterior pair of costals; lower jaw with a longitudinal symphysial ridge; epiplastra sutured or closely approximated. Plastral callosities never more than 5 and depending on environmental factors may be poorly developed even in adults. Portion of skull preceding orbits longer than orbital diameter, especially so in young specimens; postorbital arch usually one half or less than orbital diameter.

The synonymy here offered may well be divisible into recognizable subspecies but series of specimens of the presumed forms are usually lacking from areas where the variants are known. Then, too, differences in external characters (*i.e.* plastral callosities) may in a measure depend on the characters of stream beds where the animal lives, so that even series of specimens may not solve the problem completely.

Description of species: Costal plates well developed, the last pair in contact on midline. All plates of carapace strongly pitted and vermiculate. Four plastral callosities, the hyo-hypoplastral and xiphiplastral; all may be poorly developed in adult specimens. Anterior processes of epiplastra long and

slender. Epiplastra usually in contact; postorbital arch about one half of the orbital diameter, sometimes only one third of the diameter.

General coloration of young grayish to greenish, often dotted or spotted with yellow and yellow-edged black spots; dull white below. Head with yellow spotting especially on ventrolateral region; small spots on limbs.

The dark spots, usual in the young, tend to disappear completely in adult, leaving the surface a unicolored greenish gray. Spots may become indistinct on head but the intervening spaces darken, tending to form a dark network on an olive surface. Underside of head and neck, much lighter. (Description from literature.)

Remarks: The species becomes large, specimens with a carapace length greater than 700 mm being known. It is variable and certain of the variants have been named. Some of the specimens have a hyoid body copulae consisting of 3 pairs of bones, while in some there are 4 pairs. There are 2 large bony pairs of cornua attached to the 2 last members of the copulae. Certain of the specimens tend to show a slightly hump-backed condition.

Their food is chiefly of fish, crustaceans and amphibia.

These turtles are often kept in tanks of water in various shops in Bangkok where they are available for purchase. Usually younger or perhaps half-grown individuals are most frequently available. They are very vicious and one must handle them with considerable care to avoid being severely bitten, since their necks are much longer than one would suppose.

Genus **Pelochelys** Gray

Pelochelys Gray, Proc. Zool. Soc. London, 1864, p. 89 (type of genus, *Pelochelys cantorii* =*Trionyx (Gymnopus) bibroni* Owen).

Diagnosis: There are 7 neural plates. The outer part of nuchal plate overlies second dorsal rib; 8 pairs of costal plates, the last two touching mesially. Skull broad, not especially lengthened, flattened above. The postorbital arch broader than orbital diameter. Posterior border of pterygoid unattached. Hyoplastron distinct from hypoplastron. Tail very short.

Only a single species is referable to this genus. It ranges widely from Burma, throughout southern China, Indo-China, Thailand, Malaya, Sumatra, Java, Borneo, New Guinea and the Philippines. It would seem certain that this present distribution is in part due to its introduction by man since the species is widely used as food, and often carried from place to place.

Pelochelys bibroni (Owen)

(Fig. 13)

Trionyx (Gymnopus) bibroni Owen, Catalogue of the Osteological Series in the College of Surgeons, 1853, p. 185 (type-locality "Australia") (probably erroneous); M. A. Smith, Bull. Raffles Mus. Singapore, No. 3, 1930, p. 3.

Pelochelys cantorii Gray, Proc. Zool. Soc. London, 1864, p. 90 (type-locality, Malacca, Malaya); Theobald, Jour. Linn. Soc., 1868, p. 10.

Pelochelys cumingii Gray, Proc. Zool. Soc. London, 1864, p. 90 (type-locality, Philippines); Catalogue of the shield reptiles, Supplement, 1870, p. 91.

Pelochelys cantoris, Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, p. 263; Fauna of British India, including Ceylon and Burma, 1890, p. 15; Casto de Elera, Catalogue of the Fauna of the Philippines, 1, 1895, p. 406; Flower, Proc. Zool. Soc. London, 1899, p. 621; Werner, Zool. Jahrb., Band 13, 1900, p. 483; Siebenrock, Sitz-ber. Wiss. Wien, Band 111, 1902, p. 832, fig. 12; Band 112, 1903, p. 350; Zool. Jahrb., Suppl. 10, Heft 3, 1909, p. 607; de Rooij, Reptiles of the Indo-Australian Archipelago, vol. 1, 1915, p. 331 *(cantori).*

Pelochelys poljakowii Strauch, Mem. Acad. Sci. St. Petersburg (7), vol. 38, 1890, 2, p. 118 (type-locality—"Fu Tschau," China).

Pelochelys bibroni, M. A. Smith, Bull. Raffles Mus., 1930, no. 3, p. 3; The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. vol. 1, Loricata, Testudines, 1931, pp. 160-162; Mertens and Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 394.

Diagnosis: Characters of the genus.

Description of species (from a captive specimen): One of the large members of the family reaching a length above 650 mm. Orbits back from front of snout by a distance greater than their diameter. One neural plate between first pair of costals. Plates strongly sculptured with pits and depressions. The anterior parts of epiplastra short and broad, widely separated from each other; 4 well developed hyoplastral and xiphiplastral callosities in adult. Head relatively small, broad, its length about 1.75 times as long as wide. Snout short, proboscis forming only a slight projection. Carapace moderately flat, composed of a bony inner part surrounded by a wide cartilaginous border. The soft parts of carapace posteriorly crisscrossed with lines at nearly right angles to each other; laterally lines do not cross. A depressed area mesially running lengthwise of carapace.

Three inner digits of arms and legs with long strong claws, that of inner toe largest. The two outer toes not extending beyond edge of strong web or fringe which extends along leg. A small callosity at base of inner toe. A strong scalelike callosity across outer part of arm; 3 callosities in web on outer side of arm. One large elongate callosity on posterior side of leg and a heavy widened scalelike callosity on heel.

Head large, much widened in temporal region. Proboscis short, tips thick; eyes small with a dark line both in front and behind pupil. Tail short behind vent.

Color in life: Head above olive with minute black dots; carapace olive, with a few darker and lighter striations along median dorsal part; outer edge olive with small spots of darker and lighter color. Plastron flesh-colored with a few white dots on anterior parts. Chin and throat with minute dots of black and white.

Measurements in mm: Length, 350; width, 315; height of carapace, 76; length of plastron, 295; width of plastron, 290; total length, head extended, 630.

Remarks: The live captive specimen here described did well in captivity.

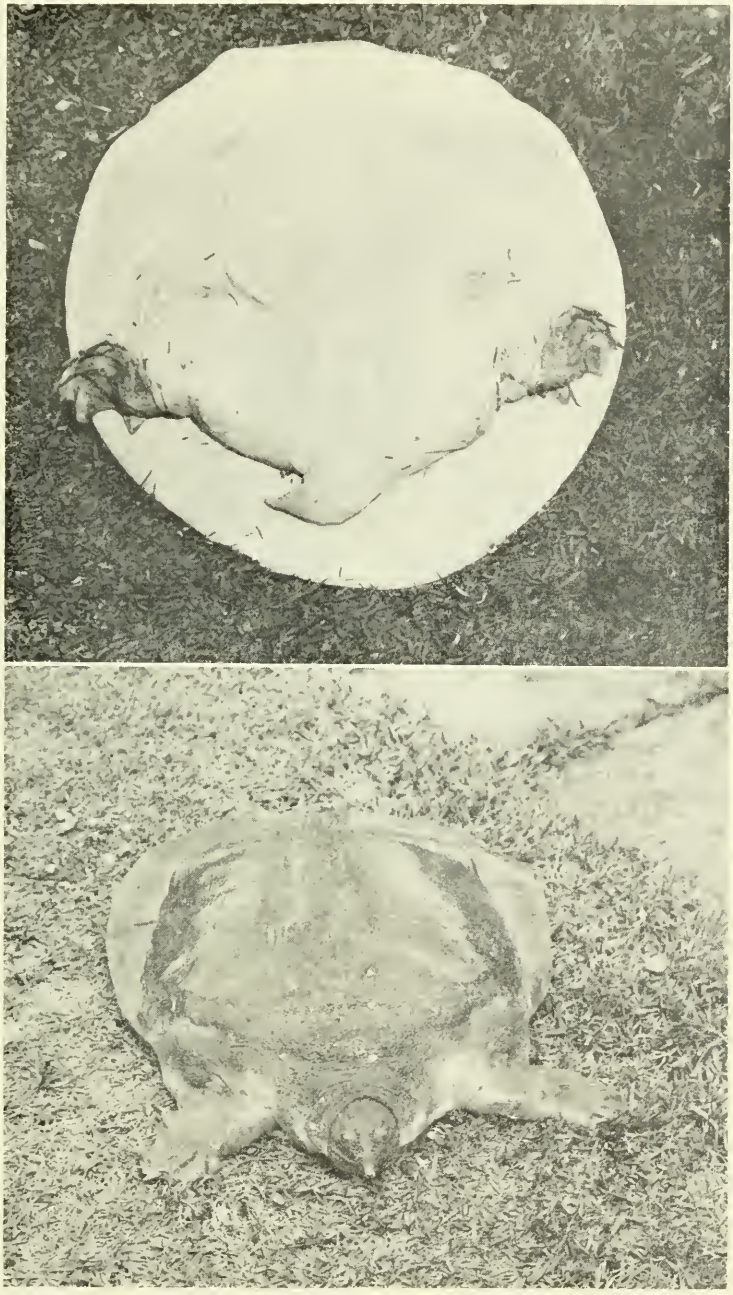

Figure 13. *Pelochelys bibroni* (Owen). Specimen living in Manila Aquarium, from San Miguel, Bulacan Prov., Luzon, P.I. Carapace length, 350 mm. Upper, ventral; lower, dorsal view.

It was kept in a tank containing two fish species *Cyprinus carpio* and *Megalops cyprinoides.* These fish were not molested. If *Ophiocephalus striatus,* the mud fish, was introduced, this was killed.

Malcolm Smith (1931a) reports 4 specimens from Central Thailand. I have examined 2 living specimens of unknown provenance in Bangkok. They were presumed to have been captured in the Chao Phraya river, in Bangkok.

Smith (1931a) calls attention to Günther's figure (1864b) stating that it represents a *Pelochelys bibroni* but with the markings of *Chitra indica!*

Genus **Chitra** Gray

Chitra Gray, Catalogue of the tortoises, crocodilians and Amphisbaenians in the collection of the British Museum, 1844, p. 49 (type of genus, *Trionyx indicus* Gray).

Diagnosis: Orbits very close to each other (the distance between them about half their diameters). Skull narrow, its length twice its width. The outer part of nuchal plate overlies second dorsal rib; 8 neural plates forming a continuous series; 8 costal scales on each side, the last pair medially in contact. Hyoplastron and hypoplastron distinct from each other. A post-orbital arch about double the diameter of orbit; posterior border of pterygoid free, without an ascending process. Tail short.

Only a single species is known in the genus.

Chitra indica Gray

Trionyx indica Gray, Synopsis Reptilium or short descriptions of reptiles, Part 1, Cataphracta, tortoises, crocodiles, and enaliosaurians, 1831, p. 47 (type-locality, Fatehgarh, Ganges "Northern India").

Trionyx aegyptiacus var. *indica,* Gray, Illustrations of Indian Zoology, vol. 1, pl. 80, 1831 (type-locality—Fatehgarh, Ganges, India); Catalogue of the shield reptiles in the collection of the British Museum, Pt. I, Testudinata (tortoises), 1855, p. 41.

Chitra indica, Gray *(part.),* Catalogue of the tortoises, crocodiles and amphisbaenians in the collection of the British Museum, 1844, p. 49; Günther, Reptiles of British India, 1864, p. 50, pl. 5 *(part.);* Boulenger, Catalogue of the chelonians in the British Museum, 1889, p. 264, fig. 70; Fauna of British India, 1890, p. 16; Annandale, Rec. Ind. Mus., vol. 7, 1912, p. 169, pls. 6 and 11; M. A. Smith, Jour. Fed. Malay States Museum, vol. 10, 1922, p. 264; The Fauna of British India including Ceylon and Burma. Reptilia and Amphibia, vol. 1, Loricata, Testudines, 1931, pp. 162-164, fig. 37; Mertens und Wermuth, Zool. Jahrb. (Syst.), Band 83, Heft 5, 1955, p. 393.

Gymnopus lineatus Duméril and Bibron, Erpétologie générale, vol. 2, 1835, p. 491.

Diagnosis: Characters of the genus.

Description of species: A very large species, the carapace reaching a length close to a meter. Head elongate, twice as long as wide; eyes placed far forward on the head. A large temporal area not roofed. Head proportionally small; snout rounded. The proboscis as long as eye opening. A single neural plate between first pair of costal bones. Dorsal plates of carapace sculptured and pitted, the anterior parts of epiplastra elongate and narrow,

widely separated from one another. Four plastral callosities. Snout rounded, with a distinct proboscis.

Carapace olive, usually with dark spots or blotches in juveniles. Adults olive, with large yellowish marks or blotches. Black-edged longitudinal streaks on neck and head, with a chevron-shaped mark just preceding disc of carapace.

Measurements: The disc of the carapace is often over 700 mm in length, reaching beyond 800 mm. Dr. Boonsong Lekagul tells me that he captured one reaching approximately a meter in length.

Remarks: This form is sought for as food in the rivers in Thailand. They are sometimes seen in the turtle tanks offered for sale. This species is widely distributed from India through southeastern Asia and Malaya. Due perhaps to its large size few are available in collections. With its large size and a vicious disposition to bite this animal must be considered dangerous to one attempting to capture it. Specimens have been reported from various localities. Besides Thailand it is known from India, Burma, and the Malay Peninsula.

Genus **Dogania** Gray

Dogania Gray, Catalogue of the tortoises, crocodiles and amphisbaenians in the collection of the British Museum, 1844, p. 49 (type of genus, *Trionyx subplanus*).

Diagnosis: Outer extremity of nuchal plate overlying second dorsal rib; 8 neural and 8 costal plates, all of the latter separated from one another by neurals. Hyoplastron distinct from hypoplastron; head large; skull convex above; postorbital arch extremely narrow, its outer margin reduced to an edge; posterior border of pterygoid free, without ascending process. Limbs exposed. Tail short.

Only a single species, *D. subplana,* is known in the genus.

Specimens I have taken are from small streams from low mountains or hills. One young specimen is from a small mountain close to Haadjai, Songkhla; the other is from a small stream at Bhetong, Yala.

Dogania subplana Geoffroy Saint-Hilaire

Trionyx subplanus Geoffroy Saint-Hilaire, Ann. Mus. Hist. Nat. Paris, vol. 14, 1809, p. 11, pl. 5 (type-locality, unknown); Gray, Illustrations of Indian Zoology, vol. 1, 1832, pl. 79; Günther, The reptiles of British India, 1864, p. 49; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History), 1889, p. 246, fig.; The fauna of British India. . . . Reptilia and Batrachia, 1890, p. 11; Flower, Proc. Zool. Soc. London. 1899, p. 619, pl. 36; Boulenger, A vertebrate fauna of the Malay Peninsula. . . . 1912, p. 9.

Trionyx frenatus Gray, Catalogue of the shield reptiles in the collection of the British Museum, 1855, part 1, p. 67 (type-locality, Singapore).

Dogania subplana, Gray, Catalogue of the shield reptiles in the collection of the British Museum, part 1, Testudinata (tortoises), 1855, p 69, pl. 33; Proc. Zool. Soc. London, 1873, p. 57, fig. 8; Annandale, Rec. Ind. Mus., vol. 7, 1912, p. 154; M. Smith, The fauna of British

India. Reptilia and Amphibia, vol. 1, Loricata, Testudines 1931, pp. 164-165; Bull. Raffles Mus., no. 3, 1930, p. 3; Mertens and Wermuth, Zool. Jahrb., Syst., Band 83, Heft 5, 1955, p. 394.

Dogania guentheri Gray, Proc. Zool. Soc. London, 1862, p. 265 (type-locality, "India").

Trionyx dillwynii Gray, Ann. Mag. Nat. Hist., ser. 4, vol. 11, 1873, p. 306 (type-locality, Borneo).

Trionyx pecki Bartlett, Sarawak Gazette, Feb. 1895, p. 30 (type-locality, Borneo).

Diagnosis: A relatively small turtle, 250 mm long; 8 neurals and 8 costals, latter separated from each other by neurals; dorsal skin with numerous longitudinal rows of short flat somewhat elongated tubercles; tail very short; dark olive with a median blackish line and 2 or 3 pairs of black spots which may be outlined in yellow. Proboscis about length of eye opening. A black line through eye running down diagonally; a A-shaped mark between orbits extending on to neck; a short median black line on occiput.

Description of species (from No. 1649, Bhetong, Yala): Carapace flat, longer than wide; anterior border a slightly recurved ridge, crenellated or denticulate; dorsal surface with 20-24 rows of rather elongate tubercles, the more median rows extending length of carapace; 8 costals distinctly outlined, being distinctly granulate or vermiculate and pitted, separated by 8 nearly parallel-sided neurals, likewise sculptured.

Plastron much shorter than carapace; xiphiplastral callosities alone distinguishable. The separation between hyo- and hypoplastra indicated by a lateral groove; head large with free flap of skin turned upward on sides of upper jaws, meeting on midline; a similar flap on lower jaws, directed downwards but not meeting mesially; interorbital distance about half length of bony part of snout; soft proboscis as long as diameter of eye. On hand, 3 claws, the inner largest; 3 claws on foot, all about same length, inner stoutest. On anterior surface of forearm, 3 narrow elongate transverse scales and on leg behind heel a single narrow curved scale, all with free edges.

Color: Blackish to brownish-olive on carapace with a black median line, with 4 rounded blackish spots, each dimly lighter on its edges; plastron whitish or grayish-white; limbs blackish above, grayish below; top of head and neck blackish; underside grayish.

Measurements in mm: Length of carapace, 177; width of carapace, 129; length of plastron, 136; greatest width of hind lobe of plastron, 92; width of head, 40.

Variation: A young specimen had the following colors in life: The plastron was generally gray-olive, the color reaching the periphery in a series of unequal, sometimes rounded, lobules separated by yellowish-brown intervals. These lobules are widest at the periphery but, narrowing quickly, terminate within a few millimeters of the edge; a median, rather ill-defined black line; 4 small black spots symmetrically spaced with scarcely any evidence of lighter edges; a few other black flecks on the carapace; under edge of posterior part of carapace is ivory; the plastron is pinkish-gray, clouded

anteriorly with darker gray; a black line from proboscis passes through eye where it turns down diagonally to a point behind the angles of the jaws. A black line extends from the frontal area to the occiput where it bifurcates, each branch running back diagonally and widening somewhat. A median black line on neck terminates in a black arrowlike mark on the occiput. The sides of neck are pinkish yellow. The top of the head and dorsal area between the black lines are olive and the lips are grayish white reticulated with darker color.

Distribution: I have seen specimens only from the provinces of Songkhla and Yala in Southern Thailand. Elsewhere it occurs in Burma, Malaya, and the Indo-Australian Archipelago. It also reaches as far east as the Philippines.

LORICATA

General Consideration of the Loricata

The crocodiles are reptilian relicts of antiquity quite as much as are the turtles. However, palaeontologists have been able to uncover more of their ancient history and perhaps more is known of their probable origin and evolution than of the turtles. All of the living forms are aquatic, living in fresh water. However, at least one form, and that occurring in our territory, is, at least, largely marine. It is to be seen occasionally along coasts, often several miles from shore presumably enroute to some fresh water lake on a nearby island or to the mouth of some river debouching into the sea. A small lake on the island of Jolo in the southern Philippines in the crater of an ancient volcano with a moderately precipitous crater rim harbors a considerable population of what is believed to be *Crocodilus porosus*.* A place was found—a path—where these animals presumably passed to the ocean which was relatively nearby.

Usually animals of terrestrial ancestry, when they take up an aquatic habitat, they do so because they are unable to obtain a sufficient quantity of food against competitors and are faced with a necessity of changing their habitat to a new food supply or becoming extinct. Usually the new habitat chosen provides food for which there is less competition and the animals will tend to adapt to new foods, and their bodies likewise adapt to the new habitat for greater efficiency in food finding.

Since these animals are easily kept and most zoos have living specimens on exhibition they are well known even to many in areas where there are now none existing in the wild. At present crocodiles are to be found on all the continents except Antarctica. The extent of their distribution is seemingly limited largely by temperature and the presence of available lakes and

* After a small disturbance was made at one edge of the lake, which is perhaps less than one-fifth mile across, some 19 were counted that came to the surface and floated.

rivers. They occur throughout Thailand in practically all suitable areas but where man has hunted them too assiduously they may have become extinct.

One of the detailed early histories of crocodiles is that of Johann Gottlob Schneider (1801). It begins with the comments of Herodotus, Pliny, Strabo, etc. and is brought down to his own time. In this work he treats of the nine known crocodiles, six of which he describes as new. Of these *Crocodylus porosus, C. siamensis* and *C. triagonatus* are still recognized under these names. His *C. longirostris* is now regarded a synonym of *Gavialis gangeticus, C. sclerops* a synonym of *Caiman crocodilus crocodilus,* and *Crocodylus oophilus* is regarded a synonym of *Crocodylus porosus.* Two of the species were from Thailand.

Duméril and Bibron in their Erpétologie Générale vol. 4, 1836, treat of the crocodiles under three groups which they call the Caimans, the Crocodiles, and the Gavials. They recognize 13 species with several varieties.

Boulenger (1889b) reviewed the crocodiles, treating them under one family, 6 genera and 22 species. One other genus, *Perosuchus* of Cope was regarded as doubtfully placed.

Mook (1921d) presented the skull and skeletal characters of the Crocodilidae in excellent detail. These were treated under 8 genera and 20 species.

Wermuth (1953) reviews the *Crocodylia* under three families: Alligatoridae with the genera *Alligator, Melanosuchus, Caiman,* and *Paleosuchus;* Family Crocodylidae with *Osteoblepharus, Crocodylus, Osteolaemus,* and *Tomistoma;* Family Gavialidae with a single genus, *Gavialis.*

Since the publication of this work very few changes have been proposed, none of which affect the forms in Thailand. In this country Malcolm Smith (1916c, p. 49) reports *Tomistoma schlegelii, Crocodylus porosus,* and *C. siamensis.* It has long been presumed that *C. palustris* was present in the country since it is known in Burma and in the southern part of the Malay Peninsula. However, Smith (1919a) asserts: "After examining a large number of crocodiles from various parts of Siam, I am convinced that it *(palustris)* does not occur anywhere in that country."

Of course, it is not impossible that they do occur and they should be looked for. Their present known distribution strongly suggests their presence at least in the upper part of the Peninsula in Thailand. The species is included in the key.

TAXONOMIC TREATMENT

SYNOPSIS OF THE THAI SPECIES OF THE CROCODYLIDAE

I. Snout 3.0 to 3.5 times as long as broad at the base; nuchal and dorsal scutes forming a single continuous shield composed of 22 transverse series, the broadest of which contain 6 scutes, the four anterior (nuchals) only 2 scutes—all keeled; 2 small occipital scutes; fingers webbed at base; outer toes extensively webbed. A

strong "crest" on the outer edge of the leg; scales on limbs keeled. Olive above with dark spots or cross-bands; length to 4.5 meters ..... *Tomistoma schlegelii*

II. Snout more than 1.5 and not more than 2.25 times as long as broad at the base; mandibular symphysis extending to the level of the fourth or fifth tooth; premaxillo-maxillary suture extended posteriorly on palate ..... *Crocodylus 2*

No longitudinal ridge in front of eye; anterior nuchal scutes (postoccipitals) well developed; a longitudinal ridge between orbits, none on snout ..... *Crocodylus siamensis*

A longitudinal ridge in front of each eye; anterior nuchal series usually absent ..... *Crocodylus porosus*

III. Snout not more than 1.5 times as long as broad at base; mandibular symphysis extending to level of fourth or fifth tooth; premaxillary-maxillary suture on the palate transverse or curved forwards; snout without ridges; dorsal shield usually composed of four longitudinal series of scutes, the median of which are broader than long ..... *Crocodylus palustris*

Genus **Crocodylus** Laurentus

Crocodylus Laurentus, Synopsis Reptilium, 1768, p. 53 (type of genus *Crocodylus niloticus*).

Crocodilus Bonnaterre, Tableau encyclopedique et Methodique des trois Règnes de la nature, Erpétologie, 1789, p. 32; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History), 1889, p. 277.

Champse Merrem, Vers. Syst. Amph., 1820, p. 36; Werner, Loricata, Das Tierreich, Lief. 62, 1933, pp. 1-40.

Tomistoma S. Müller, Arch. Naturg. Berlin, 1846, Band 12, p. 122; Krefft, Proc. Zool. Soc. London, 1873, p. 334.

Gray has recognized several other nominal genera: *Mecistops, Oophilus, Palinia, Molinia, Bombifrons, Temsacus, Philas.* These generally have been regarded as synonyms of *Crocodylus.*

Crocodylus siamensis Schneider

(Fig. 14)

Crocodylus siamensis Schneider, Historiae amphibiorum naturalis et literariae, fasc. 2, 1801, p. 159 (type-locality, Siam); Günther, Reptiles of British India, 1864, p. 61, pl. 8, fig. b; Strauch, Syn. Crocod., 1866, p. 50; Boulenger, Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum, London, 1889, p. 282; M. A. Smith, Nat. Hist. Soc. Siam, vol. 3, 1919, p. 217, 3 pls.; Bull. Raffles Museum, no. 3, 1930, pl. 1; Wermuth, Mitteil. Zool. Mus. Berlin, Band 29, Heft 2, 1953, pp. 481-483, figs. 48, 49.

Crocodilus galeatus, Cuvier, Ann. Mus. Hist. Nat. Paris, vol. 10, 1807, p. 51, pl. 1, fig. 9; Duméril and Bibron, Erpétologie Générale, vol. 3, 1839, p. 113.

Crocodilus vulgaris, Schlegel and Müller *(part.) in* Temminck, Ver. Nat. Gesch. Nederland Indies, Rept. 1844, p. 28, pl. III, fig. 9.

Crocodilus palustris, Laidlaw, Proc. Zool. Soc. London, 1901, p. 58 (Patani).

Bombifrons siamensis, Gray, Ann. Mag. Nat. Hist., ser. 3, vol. 10, 1862, p. 269.

Diagnosis: A total of 17 or 18 teeth on each side of upper jaw, 4 or 5 of which are on each premaxillary; snout less than twice as long as wide at base.

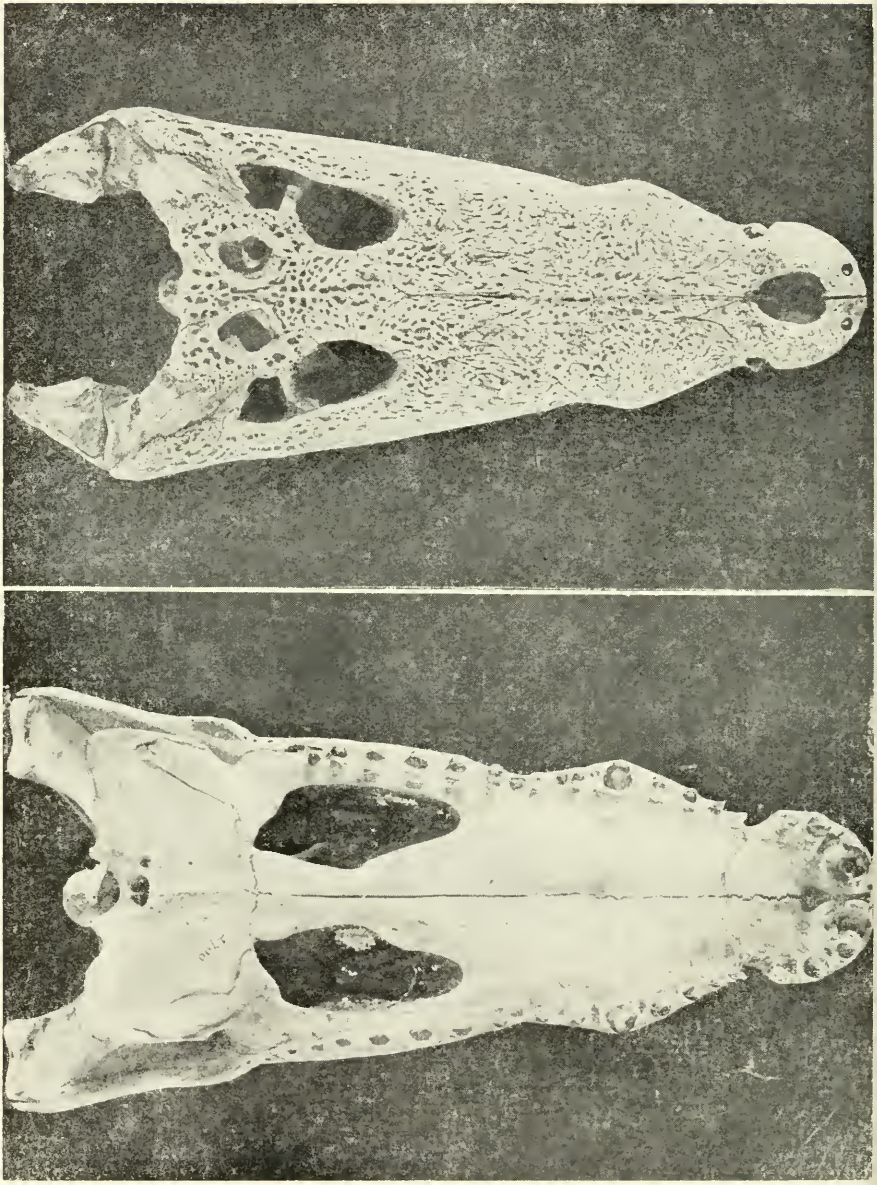

FIGURE 14. *Crocodylus siamensis* Schneider. Skull. From upper, dorsal; lower, ventral view.

On nuchal region, usually if not invariably, two large pairs of scutes each bordered laterally by a single enlarged scute. Preceding these a transverse row of 4 somewhat smaller scutes separated well from the nuchals. Olive to brownish above; whitish or yellowish below. Young specimens may be black-spotted. A serrate fringe on outer side of limbs.

Description of species: Dorsal surface of snout relatively smooth, area about nostrils somewhat elevated, Area preceding and between eyes definitely concave, the cranial table nearly square, slightly concave. Posterior to cranial table scales small, transversely arranged. There follows four rather enlarged scutes separated mesially, all keeled; following several transverse rows of very small scales are two pairs of much enlarged scutes making contact mesially with a single much enlarged scute lateral to each of these pairs. On dorsum of body, 16 or 17 transverse rows of enlarged scutes in six longitudinal series, the bony portion of the scutes contiguous with one another. The number of scutes in the transverse rows reduce to 2 on the tail for some distance.

The skull has 17 or 18 teeth on both sides of the upper jaw, 4 or 5 confined to the premaxillary; the premaxillo-maxillary suture curves backwards. The snout is 1.5 to 1.66 times as long as wide measured just in front of orbits. A distinct ridge runs forward a distance anterior to the orbits, converging slightly. A small poorly developed ridge in interorbital region usually present. The mandibular symphysis extending to fourth tooth.

Color: Usually olive or greenish olive to brown, somewhat variegated. The young usually spotted black, and generally paler above. The tail is banded in black.

Measurements: The species is known to reach a length of 3.5 meters and may even reach 4 meters. The tail constitutes approximately half the length.

Distribution: The species occurs in Thailand both in the central part and in peninsular areas. There are reports that the species is common in the river Quae (Quae Noi), Western Thailand. (from literature).

Remarks: Malcolm Smith (1919a), who has made the greatest contribution to the herpetological knowledge of Thailand, gives a detailed account of this species (pp. 217-220).

Crocodylus porosus Schneider

(Fig. 15)

Crocodilus porosus Schneider, Historiae amphibiorum naturalis et literariae, fasc. segundus, 1801, pp. 159-160 (type-locality not given); Gray, Catalogue of the tortoises, crocodiles, and amphisbaenians in the collection of the British Museum, 1844, pp. 1-40. Günther, Reptiles of British India, 1864, p. 62, pl. 7; Boulenger, Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum, 1889, pp. 284-285.

Crocodilus oophilus Schneider, Historiae amphibiorum . . . fasc. segundus, 1801, pp. 165-166.

Crocodilus biporcatus raninus Schlegel & Müller, Verh. Nat. Gesch. Nederl. Besitt., Rept., 1844, p. 28.

Oophilus porosus Gray, An. Mag. Nat. Hist., ser. 3, vol. 10, 1862, p. 267; Trans. Zool. Soc., vol. 6, 1867, p. 138; Catalogue of the shield reptiles, 1872, pt. 2, p. 8.
Crocodilus pondicerianus Gray, Ann. Mag. Nat. Hist., ser. 3, vol. 10, 1862, p. 267; Günther, Reptiles of British India, 1864, p. 62, pl. 7.

Diagnosis: Head somewhat triangular, relatively short. A pair of ridges extending forward on the skull between eyes, then curving slightly outward and then inward, the discontinuous ridges converging slightly; 3 large nuchals, often not contiguous, on each side; usually no enlarged occipital scutes preceding nuchal scutes.

Description: A very large species, reputedly reaching a length rarely of about 10 meters. Snout moderately long, narrowed back of level of nostrils, elevated somewhat near tip. Cranial table somewhat concave as are interorbital areas. No enlarged postoccipital scutes (except occasionally in young specimens, and some Ceylonese specimens may have 2 or, more rarely, 4). Dorsal scutes in 16-17 transverse rows and 6 to 8 contiguous or nearly contiguous longitudinal series, the scales regular, separated from the enlarged nuchals, all keeled. Enlarged nuchals, 4 to 6 slightly separated or contiguous, the four median forming a square. Most lateral scales and those on limbs keeled. Fingers webbed at base; toes with much web. A fringe of scutes on outer posterior part of leg.

Skull with 17 to 19 teeth in upper jaw; mandibular symphysis extending to fifth tooth; premaxillomaxillary suture on palate directed backwards or W-shaped. Nasal bones separating the premaxillaries above.

Color: Generally dark olive dorsally. The young specimens are lighter, usually spotted with black. Small dots on head. Venter yellowish.

Measurements of skull in mm: Tip of snout to supraoccipital 642; tip of snout to end of quadrates, 721; length of snout, 464; skull width across quadratojugals, 369; width of cranial table (posterior end), 177; width at base of snout, 220; width across narial opening, circa 158; length of mandible, 785; width of mandible, 390 (American Mus. No. 15179). (from Mook 1921d).

Remarks: Crocodilus porosus grows to a known size probably greater than other living Crocodilia. Smith (1931a) reports one from northern Queensland measuring 9 meters 70 cm (about 32 feet). Another report, perhaps less well authenticated, reports one with a probable length of 33 ft! Barbour (1924a) reports a Philippine specimen with a length of 29 ft., a girth behind forelimbs of 11 ft., and a skull 34.75 in. long (now in Mus. Comp. Zool., Harvard College).

A specimen captured in the mouth of a Batangas river debouching into Manila Bay was captured by General Aquinaldo. I had the 18 foot specimen mounted for exhibition, but it was later destroyed at a fire at the Manila Carnival where it was temporarily on exhibition.

For the most part *C. porosus* prefers salt water and usually occupies the river mouths and coastal waters. They are often seen swimming at sea and

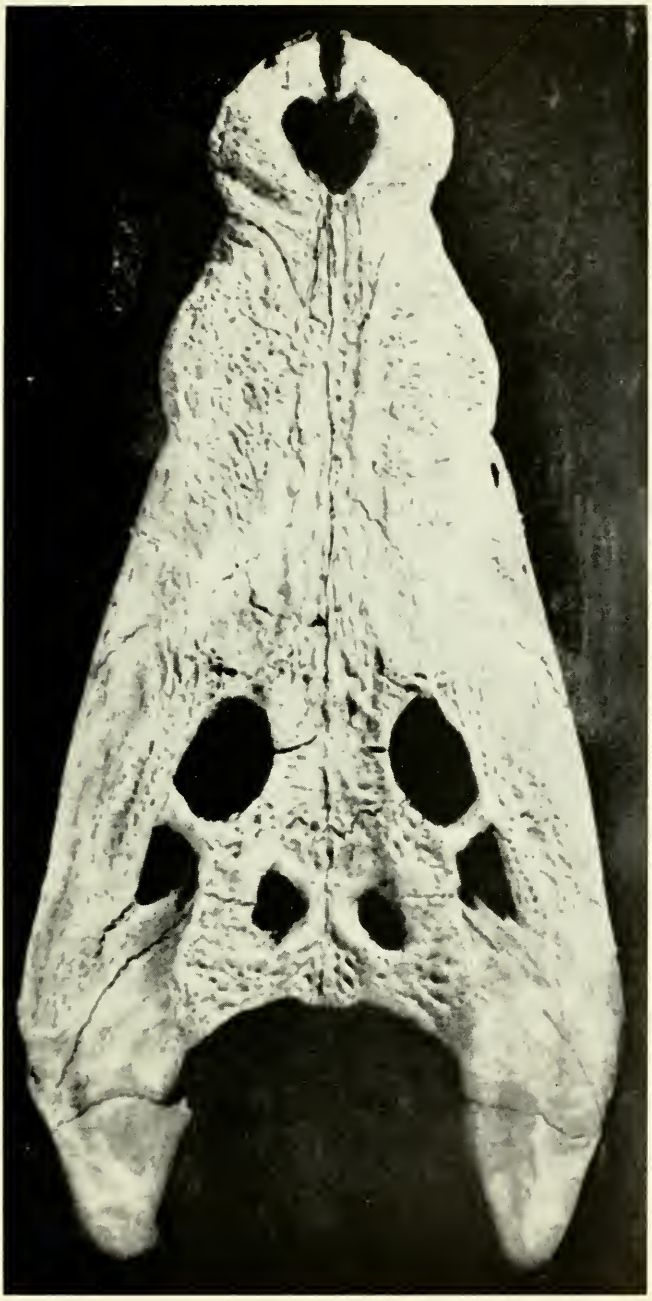

Figure 15. *Crocodylus porosus* Schneider. Amer. Museum Nat. Hist. No. 15179. Skull length, 642 mm. From Mook (1921a, fig. 4).

have been reported 40 miles from the nearest land. As a result of this habit the species has spread more widely than other crocodiles. One of course cannot rule out the possibility that they may have also been transported by man. They are known from estuaries of Thai rivers, Gulf of Thailand, Coasts of India, Ceylon, Philippines, Vietnam, Cambodia, Hong Kong, Solomon Islands and Fiji, and some Indo-Australian Islands.

Karl Schmidt (1928a) has reported the species as being seen in fresh water 60 miles from the sea. M. L. Smith (1931a) believes that in Thailand they normally do not ascend rivers and are normally inhabitants of the mouths of muddy rivers. Smith calls it the "Estuarine Crocodile."

Genus **Tomistoma** S. Müller

Crocodilus S. Müller, Tijdsch. Nat. Gesch., Amsterdam and Leiden, 1838, vol. 5, p. 17.

Mecistops (part.) Gray, Catalogue of tortoises, crocodiles and amphisbaenians in the collection of the British Museum, 1844, p. 57.

Tomistoma S. Müller, Arch. f. Nat., 1846, p. 122; Gray, Catalogue of shield reptiles in the collection of the British Museum, Pt. II, Emydosaurians, rhynchocephalians, and amphisbaenians, 1872, p. 6; Boulenger, A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore, Reptilia and Batrachia, 1912, pp. 3-4; Mook, Bull. Amer. Mus., vol. 44, 1921, p. 140; Wermuth, Mitt. Zool. Mus. Berlin, Band 29, Heft 2, Dec. 1953, pp. 500-501; Mertens and Wermuth, Zool. Jahrb. (Syst.), 1955, Band 85, Heft 5, p. 412.

Rhynchosuchus Huxley, Jour. Proc. Linn. Soc. Zool., vol. 4, p. 16, 1859.

The type of the genus is *Tomistoma schlegelii* S. Müller. The species occurs on the Asiatic mainland as far north as southern Thailand. It is known on the islands of Borneo and Sumatra, and doubtless occurs on certain other Indonesian islands.

Diagnosis: Snout long, narrow; four longitudinal series of juxtaposed keeled bony scutes on the back. There are 20 to 21 premaxillomaxillary teeth; 18 to 19 dentary teeth, the latter received into interdental pits; fifth maxillary tooth largest, lateral. First and fourth dentary teeth fit into upper jaw notches; nasal bones do not reach the nasal openings by a considerable distance but are in contact with the premaxillaries for some distance. Nasal opening somewhat pear-shaped, not as large as the supratemporal fossa; a small palpebral bone.

Dentary bones slender, forming a common suture back to level of contact with the splenials, the suture being continued one third farther back between the splenials.

Tomistoma schlegelii (S. Müller)

(Figs. 16-17)

Crocodilus (Gavialis) schlegelii S. Müller, Tijdsch. Nat. Gesch., vol. 5, 1838, p. 77 (type-locality, South Borneo).

Tomistomia schlegelii S. Müller, Archiv. für Naturg., Band 12, 1846, p. 122; Boulenger, Catalogue of the chelonians, rhynchocephalians, and amphisbaenians in the British Museum, 1889, p. 276; Proc. Zool. Soc. London, 1896, p. 628; Flower, Proc. Zool. Soc. London,

1899, p. 622; Butler, Jour. Fed. Malay States Mus., vol. 1, 1905, p. 1; Boulenger, A vertebrate fauna of the Malay Peninsula . . . Reptilia and Batrachia, 1912, pp. 3-4; Mook, Bull. Amer. Mus. Nat. Hist., vol. 44, 1921, pp. 140-151, fig. 2 (skeletal study); Wermuth, Mitt. Zool. Mus. Berlin, Band 29, Heft 2, 1953, pp. 501-503, figs. 63 (head) 64, skull; Mertens and Wermuth, Zool. Jahrb. (Syst.), 1955, Band 83, Heft 5, p. 412.

Diagnosis: Characters of the genus.

Description: From a juvenile specimen (unnumbered) Chulalongkorn Univ., from Southern Thailand. May 10, 1958. Prepared skull, and literature.

Head slender, the snout extended greatly; the width of the snout at middle, about 9 or 10 times, in its length (to last tooth or front level of orbit), the snout widening in front of orbits; upper jaw extending several millimeters beyond the dentaries, the two terminal teeth directed straight downward; postoccipital scutes small, in several indefinite, inconspicuous rows; six nuchals forming two rows of paired scales, seemingly not separated from the dorsals; body with a dorsal squamation consisting of a longitudinal series of juxtaposed bony scutes extending from the nuchal region, composed of 22 transverse series, of from two to six scales in width. Two small postoccipital scutes. A well-developed basal web on toes; fingers webbed at their base. A crest bordering outer edge of leg. Scutes on legs and arms keeled.

Color: Generally dull olive or greenish, with dark brown spots. Posterior dorsum and tail sometimes with transverse bands and spots; whitish beneath; iris yellowish brown.

Measurements in mm: Total skull length including jaws, 260; length of skull, snout tip to condyle, 227; skull to front edge of orbits, 75; snout, front of orbits to snout tip, 164; width of snout in front of orbits, greatest, 40; narrowest width preceding orbits, 14; length of orbit, 28; greatest skull width, 79; length of lower jaws, 254.

Mook gives measurements in mm of a skull (American Museum no. 15177), as follows: Snout tip to supraoccipital, 765; to end of quadrates, 842; snout length, 577; length of lower jaw, 935; width interorbital space, 40; width across quadratojugals, 352.

Adults are said to reach a length of about 17 ft.

Distribution: In Thailand the species has been taken only in the southern part. The type-locality is the Perak river close to the southern border of Thailand. Specimens have been taken in Borneo and Sumatra. It most probably occurs on some of the other islands of the Indo-Australian Archipelago.

Remarks: The species is reputed to feed chiefly on fish and has not been known to attack human beings.

Tomistoma shows a strong resemblance to *Gavialis* of India. Despite the fact that they have been associated with *Gavialis* by various authors, it would appear that it is actually a member of the family Crocodilidae rather than Gavialidae.

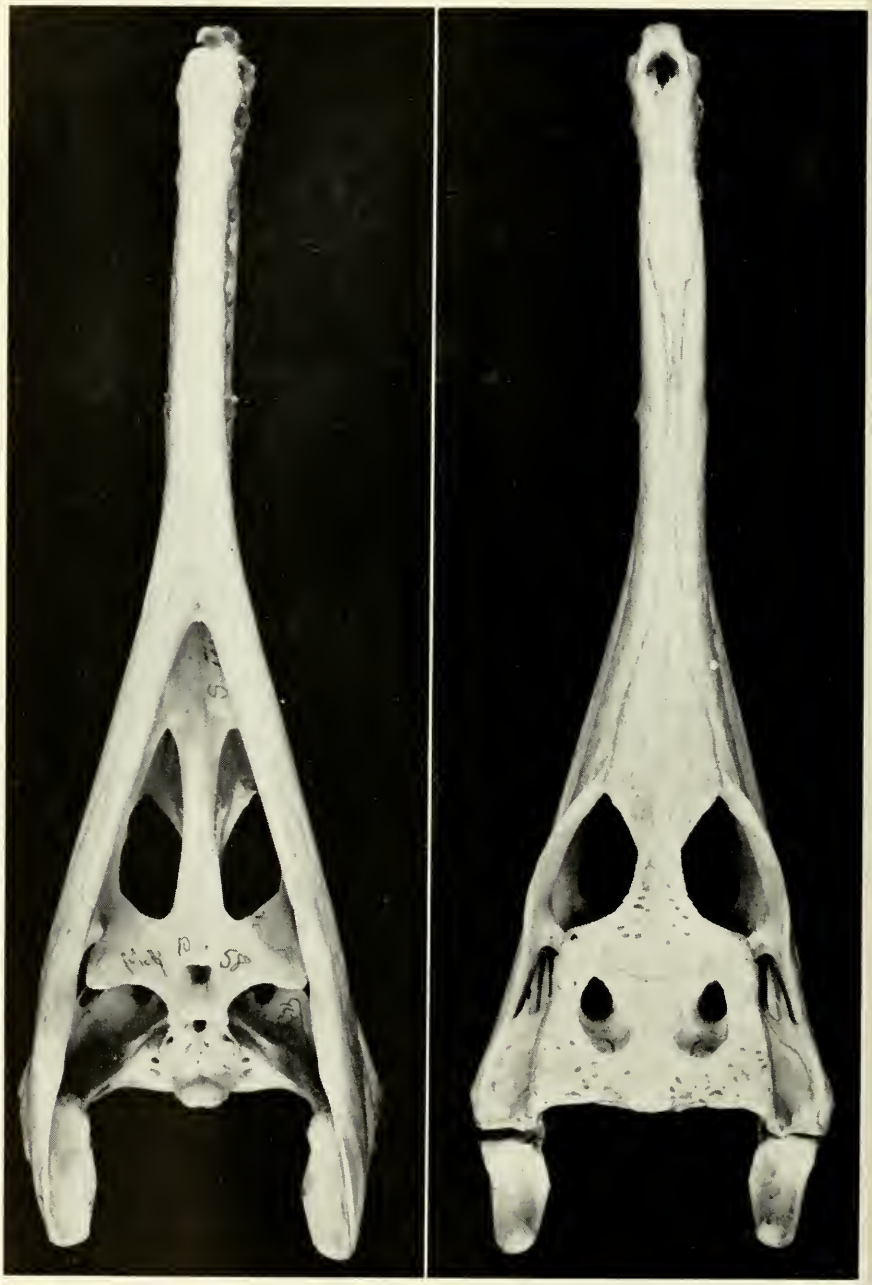

FIGURE 16. *Tomistoma schlegelii* S. Müller. Chulalongkorn Univ. No. 58 (young). "Southern Thailand." Actual skull length, 260 mm. Ventral view, left; dorsal view, right.

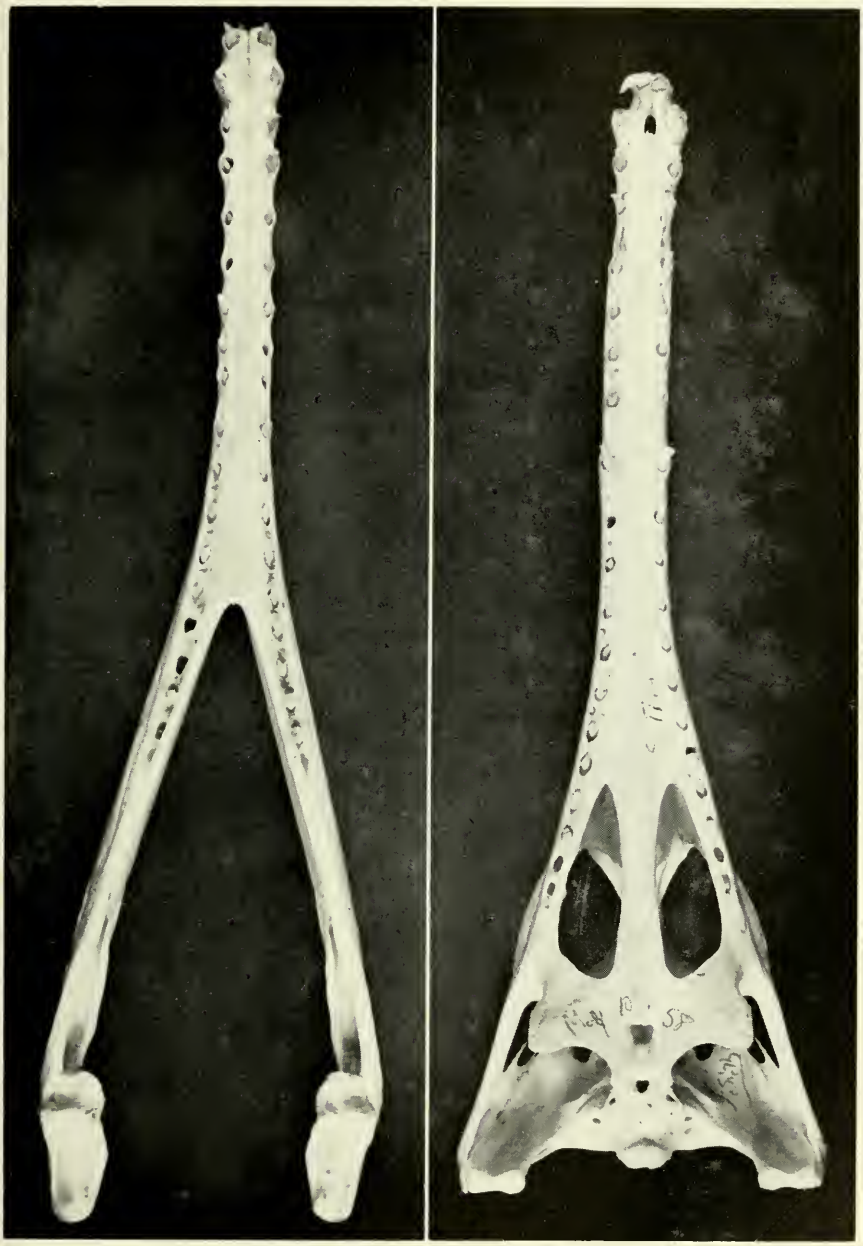

Figure 17. *Tomistoma schlegelii* S. Müller. Chulalongkorn Univ. No. 58 (young). "Southern Thailand." Left, upper view of lower jaw; right, ventral view of skull. Skull length, 260 mm.

The skull of *Tomistoma* may easily be distinguished from *Gavialis,* having the maxillary bones in contact for nearly half the length of the snout. In *Tomistoma* the maxillaries are completely separated by contact of the premaxillaries and nasals.

Mook (1921d) writes: The characters of the genus *(Gavialis)* differ widely from those of other living crocodilians. In spite of the fact that *Tomistoma* is in many respects intermediate between this genus and *Crocodilus* there is no appreciable graduation in characters between the gavial and the true crocodiles, *Tomistoma* being much closer to crocodiles than to *Gavialis.*

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A BIOSYSTEMATIC STUDY OF THE SUBGENUS *SELFIA* OF *CULICOIDES* (DIPTERA: CERATOPOGONIDAE)

By

William R. Atchley

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A Biosystematic Study of the Subgenus *Selfia* of *Culicoides* (Diptera: Ceratopogonidae)[1]

William R. Atchley

ABSTRACT

The subgenus *Selfia* is a sibling species complex of biting midges restricted to western North America. These flies exhibit complicated patterns of geographic variation and offer an excellent opportunity to examine intra- and interspecific relationships in several closely related species.

Large samples of reared and associated larvae, pupae and adults were employed to analyze the morphology, taxonomy and biology of the seven species of *Selfia*. Geographic variation and natural hybridization among *C. (S.) hieroglyphicus, C. (S.) denningi* and *C. (S.) jamesi* were examined by generalized discriminant function and principal components analyses. Geographic variation in 16 adult female characters and 10 from males was studied by generalized discriminant functions in the 3 forms. Analysis of variance indicates significant interpopulational variation exists in all of these characters except the number of antennal sensory pits in males of *denningi*. The discriminant function results were compared with those obtained from a principal components analysis using 45 pupal and adult characters in the females and 36 in males. In general, the projection of population means onto the first 3 principal components complemented the relationships shown by discriminant functions. However, since the pupal stage is included, the principal components analysis sometimes gave results inconsistent with those of the discriminant function method.

Variation in *denningi* was found to be one of size with those populations from lower elevations and more southern parts of the range being smaller than their counterparts in cooler areas. In *hieroglyphicus,* similar results were obtained, although variation is not in as orderly a clinal pattern as found in *denningi*. The situation in *jamesi* is quite complex due to occurrence of natural hybridization with *denningi* and *hieroglyphicus*.

Substantial statistical and biological evidence indicates that a natural zone of hybridization occurs between *jamesi* and *denningi* at several localities in Montana, Wyoming, Nevada and Utah. Variation in a number of characters was examined statistically for several hybrid populations and certain structures, e.g., the number of spiracular openings the pupal respiratory horn, appear to show dominance toward the *jamesi* condition. The possible occurrence of introgression in a Sublette Co., Wyoming population is discussed. Evidence is presented of hybridization between *jamesi* and *hieroglyphicus* along altitudinal gradients at two localities in Utah and New Mexico.

Data from a large number of localities would indicate that larvae of *hieroglyphicus* and *jamesi* are distinguishable. Larvae of *denningi* are similar to those of *jamesi* but are smaller. Pupae of *denningi* and *jamesi* are distinguishable by the number of spiracular openings on the respiratory horn. Pupae of *hieroglyphicus* are distinguishable from those of *jamesi* and *denningi* by the number of spiracular openings on the respiratory horn and by the number of dorsal abdominal setae.

[1] Contribution No. 1438 from the Department of Entomology of The University of Kansas.

phicus are generally associated with small to medium-sized, fresh to alkaline, warm water streams. The larvae of *jamesi* would seem to have the broadest ecological tolerances of any the *Selfia* species, having been reared from small to large, fresh water, alkaline and polluted streams with cold to warm water. These two species replace each other along an altitudinal gradient with *hieroglyphicus* found at lower elevations and *jamesi* at higher elevations. *Culicoides denningi* was reared from habitats ranging from a very cold, swift river to a small, stagnant stream; however, *denningi* would appear to be most abundant in larger, cold water streams. *Culicoides jacksoni* was reared from two geographically disjunct localities but each locality shared several common features. Each was a cold, high altitude pool formed immediately above a waterfall. The affect of rate of flow of a stream, wind and substrate on the microdistribution of the immature stages of the various species is discussed.

A number of peculiar modifications of the reproductive system, e.g., the elongate, slightly sclerotized spermathecae in the females, eversible aedeagus in males of the *hieroglyphicus* and *jacksoni* groups, etc., make *Selfia* unique among *Culicoides.* However, with the exception of the unusual respiratory horn and abdominal spines and setae in pupae of *brookmani,* the immature stages of *Selfia* are much like other *Culicoides. Selfia* shows greatest morphological affinity to a small, primitive group of Old World *Culicoides* centered around *sejfadnei,* but also considerable similarity to the genus *Stilobezzia.*

INTRODUCTION

The subgenus *Selfia* of *Culicoides* is a sibling species complex of biting midges which has long been a problem to students of ceratopogonids. The absence of distinguishing features in the females, such as a pattern of wing spots or a well-sclerotized spermathecal system, has intensified the difficulties.

This study was approached according to the concept of "holomorphology" (*sensu* Hennig). Large samples of reared and associated larvae, pupae and adults were employed to analyze the morphology, cytology, taxonomy and geographic variation of this group. These analyses were then superimposed on field studies of the ecology and biology of the immature stages to arrive at a number of conclusions. This method has much to offer toward the ultimate analysis of any taxonomic problem, considerably more so, in my opinion, than such rather one-sided approaches as numerical taxonomy.

There has been only one other attempt to critically analyze geographic variation in *Culicoides,* and this was done in terms of subspecies (Wirth and Jones, 1957). Further, this study of *Selfia* represents the first attempt to make extensive use of the immature stages in the solution of a complex problem. It would seem that the methods used here could be profitably extended to such problem groups as the *piliferus* or *obsoletus* complexes.

After my original encounter with the species of *Selfia* in a study of the

Culicoides of New Mexico, I was convinced that the solution to this problem lay in the selection, by generalized discriminant functions, of a combination of characters to separate the females of the various species. After three years and a considerable expenditure of funds for computer time, it is now evident that the *Selfia* problem does not have a "solution" as such, but rather an explanation.

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MORPHOLOGY

The general morphology of *Culicoides* has been described by Carter, Ingram and Macfie (1920), Tokunaga (1937), Lee (1948), Wirth (1952), Wirth and Blanton (1959) and Atchley (1967). General aspects of the head were examined by Snodgrass (1944); more detailed studies have been reported by Jobling (1928) on *C. pulicaris, C. obsoletus* and *C. vexans,* and Gad (1951) for *C. impunctatus.* The genitalia were the subject of an early Russian paper by Pomerantzev (1932), and Megahed (1956) reported on the anatomy and histology of the alimentary canal of *C. nubeculosus.*

The most complete work of the morphology of the immature stages of any species of *Culicoides* is that of Lawson (1951) on *C. nubeculosus;* however, there are a number of additional ones which, although not as

complete as Lawson's, are of considerable importance. These include Kettle and Lawson's (1952) study on the immature stages of British *Culicoides* and allied genera. In North America, there have been several studies of varying detail of the immature stages, particularly the pupae. Among the more important of these are those of Jones (1961a), Linley and Kettle (1964), Linley (1965), Thomsen (1937), Williams (1951) and Wirth (1952a,b). The terminology of pupal body chaetotaxy used in this paper follows Carter *et al.* (1920), and that of the larval head capsule is from Lawson (1951).

The following is a detailed account of the morphology of the subgenus *Selfia,* particularly the male and female reproductive systems. I have attempted to discuss the morphological modifications in the various regions of the body of the adult, pupa and larva, and in a later section I shall try to relate these findings to phylogeny. The head and thoracic regions of *Selfia* bear a close resemblance to those of other subgenera of *Culicoides.* Consequently, much of what is said about these regions in *Selfia* would pertain to other infrageneric groupings. The abdomen, however, particularly the reproductive systems, contains a number of modifications found only in this subgenus.

Adult: *Head*

The evolution of the head capsule in Diptera can be thought of as having occurred in two principal patterns: one of consolidation of the head segments with the subsequent loss of sutures and the other of membranization of certain areas, e.g., in *Culicoides* the antennal region and the posterior side of the head. Consequently, the delimitation of various head segments is difficult without reference to musculature.

The hypognathous head of *Selfia,* as of other *Culicoides,* is a subspherical structure with the most prominent parts of the facial region being the outwardly projecting antennae and the elongate proboscis (Fig. 1). The lateral region is composed of the large, reniform compound eyes which, in females of *Selfia,* are always separated dorsally by the narrow dorsal projection of the frons. The broad flattened setigerous vertex occupies most of the dorsum of the head and can be arbitrarily delimited from the frons by the transverse interocular suture. The latter is not an intersegmental line but rather a secondary reinforcement to add support to the frontal area of the head; however, it still serves as a useful landmark. When the eyes are contiguous, as in males of *Selfia* and females of other species groups, the fused margins of the compound eyes can be thought of as the boundary between the frons and vertex. In the taxonomic section, the extent of separation of the eyes was obtained by measuring the distance from the interocular suture to the margin of the eyes above the ocelli. This distance was divided by the narrowest distance between the eyes.

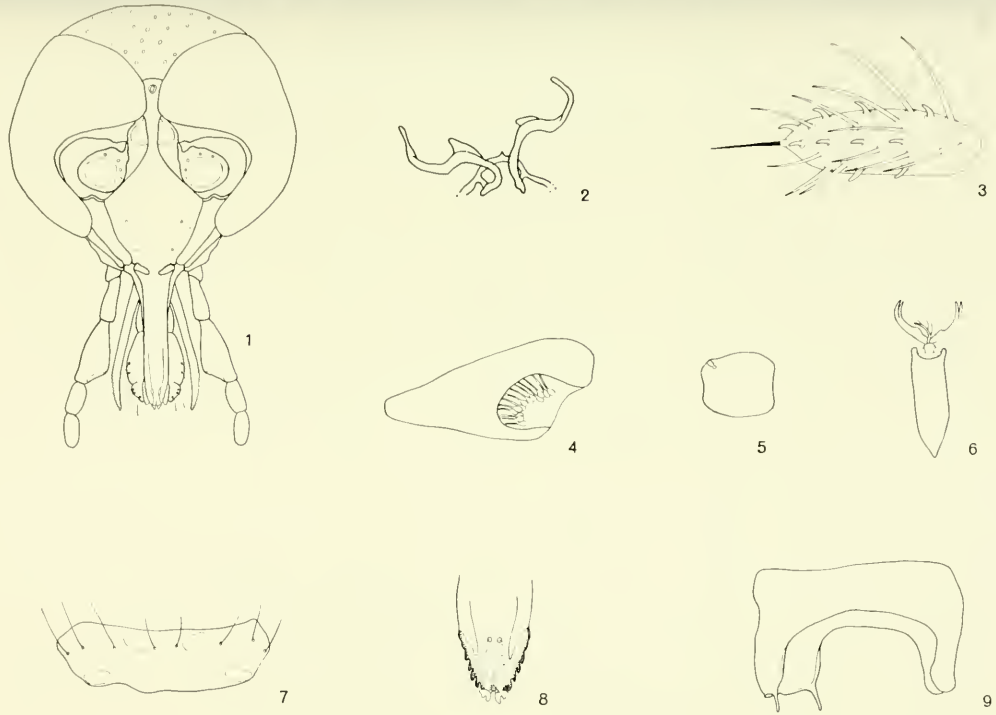


Fig. 1. Head of female *C. multipunctatus*. Fig. 2. Cervical sclerites of *C. denningi*. Fig. 3. Terminal flagellomere of *C. tenuistylus* female. Fig. 4. Third maxillary palpal segment of female *C. hieroglyphicus*. Fig. 5. Fourth antennomere of female *hieroglyphicus*. Fig. 6. Pre-tarsal claw of male *hieroglyphicus*. Fig. 7. Eighth abdominal tergum of female *hieroglyphicus*. Fig. 8. Tip of labrum of female *denningi*. Fig. 9. Lateral view of ninth abdominal segment in male *hieroglyphicus*.

The facial region is composed primarily of the fused frons and clypeus, the frontoclypeal suture being apparently lost during the consolidation of the head sclerites. That portion of the frontoclypeus corresponding to the frons, together with the genae, circumscribes the antennal bases and extends posteriorly between the eyes. Lying just posterior to the proboscis is the clypeus, a broad, convex region with strongly recurved outer margins. The clypeus is joined to the labrum-epipharynx by a pair of small sclerites, the tormae. The genae are a pair of slender sclerites extending from the anterior tentorial pits to the extension of the frons bordering the mesal edge of the compound eyes. Arising from the genal infolds is a pair of elongate, stout rods that lie beside the outer edges of the clypeus and on which the basal end of the mandible articulates. These rod-like sclerites are referred to as the mandibular arms (mandibular condyles *sensu* Jobling).

The compound eyes are many-faceted structures lacking interommatidial pubescence. The two ocelli are small, rather indistinct, setose lobes lying along the outer margins of the dorsal projection of the frons just below the compound eyes.

The posterior part of the head consists of the large U-shaped occiput ventrally fused to the postgenae. The foramen magnum is a large opening consisting of two arches, a dorsal one set off from the principal, but incomplete, ventral arch by a pair of mesally projecting occipital condyles. The ventral arch is incomplete in that it is bounded along its lower margin by membrane. The cervical sclerites are long, sinuate structures generally with a lateral projection (Fig. 2).

The antenna is composed of 15 units: the scape, which is a flattened, ring-shaped segment with a dorsal, thumb-like projection and a number of long setae; an enlarged, globular pedicel, which is considerably larger in the males and contains scolopophorous sensilla, the Johnston's organ; and a flagellum composed of 13 flagellomeres. (In the taxonomic section the antenna is divided into 15 "antennomeres" for simplicity in describing and discussing the distribution of various sensory organs. This is done to retain continuity with other taxonomic papers since previous authors, myself included, have referred to the first flagellomere as the third "segment" or "antennomere.") The proximal eight flagellomeres of the females are always slightly longer than wide, the basalmost one always longest, while the distal five are much longer than wide. In the males the first ten flagellomeres are slightly longer than wide and have a dense whorl of long setae giving the antenna a plumose effect. The distalmost three flagellomeres are rather prolonged but have only a few long setae. The antennal ratio in females is obtained by dividing the total length of the last five flagellomeres by that of the first eight.

There are at least five different types of sensorial organs present on the

antennae. One of these, the scolopophorous Johnston's organ, is confined to the pedicel. The second is the sensillum coeloconicum; these are black and goblet-shaped (Fig. 5). They are located only on the second flagellomere opposite the olfactory pit and are found in both sexes. The third category of antennal sensory organs are the so-called "olfactory pits," sunken sensilla visible as pits surrounded by numerous setulae. They are always found on the first flagellomere and in a more or less regular pattern on the next nine. In *Selfia* they are not present on the distal five flagellomeres. These pits are more numerous in females, and Jamnback (1965) has introduced circumstantial evidence indicating the number of such pits in the females is related to host preferences. Those species which are ornithophilic appear to have more olfactory pits than do mammalophilic forms. The term "antennal sensory pit" in the remainder of this paper refers to this type of sensillum.

The fourth type of sensillum is a long, tapering, slightly curved filament found on all of the flagellomeres. They are very lightly pigmented structures arising from clear areas on the flagellomere. At no time do they arise from sockets as do setae. The number of these sensilla varies depending upon the species and also the flagellomere examined. Some species, e.g., *multipunctatus,* have three on each of the proximal eight flagellomeres, while others, such as *jamesi,* have only two. Further, the number is markedly increased on the apical five flagellomeres, with twelve or more on the terminal one (Fig. 3). On the proximal flagellomeres one such sensillum is usually much shorter than the other(s) on the same flagellomere.

The final type of sensillum resembles the fourth, in that it is very lightly pigmented and arises from clear areas of cuticle, but differs in being much shorter, distally rounded and restricted to the distal portion of the proximal five flagellomeres in the females.

The latter two types of sensilla, particularly the fourth, also occur in the Leptoconopinae (Atchley and Wirth, MS. in prep.) and Forcipomyinae (Wirth, 1952a) and in the past have been referred to as "hyaline sensory filaments."

The mouthparts of the females are well developed, and non-haematophagous forms, such as illustrated by Jamnback (1965) for other groups of *Culicoides,* do not occur in *Selfia.* The biting apparatus consists of the labrum-epipharynx, mandibles, maxillae, labium and hypopharynx. The sucking apparatus is composed of a cibarial and pharyngeal pump. The labrum is an elongate structure with approximately eight distal teeth, the number depending on the species (Fig. 8). There are usually two subapical clear areas on the labrum which, with phase contrast microscopy, can be seen to give rise to minute hairs reputed to be sensilla. The labrum can be shown to be composed of two regions or parts. The median part bears a pair of teeth at the apical end and is basally slender, extending into the head

where it forms a point of attachment for the labral muscles. The lateral part possesses a number of apical denticles referred to as the lateral teeth. There is some disagreement in the literature on *Culicoides* as to which of these labral parts is joined to the tormae. Jobling showed the lateral part to be united to the tormae, while Gad opined that it was the median part and illustrated the tormae in contact with this portion. The labrum of *Selfia* supports Jobling's hypothesis and closely approximates his illustrations for these structures. The males have the labrum much shorter and lacking in denticulation. Instead of teeth, the labrum of the males bears a number of short bristles.

The mandibles are much like those of other species of *Culicoides,* being long and blade-like in the females, with a number of distal teeth and articulating basally against the mandibular arm. The mandibles in *Culicoides* have been shown to have an interlocking device so as to give them a scissors-like action. The males have shorter mandibles, which are distally pointed and devoid of teeth.

The maxilla consists of three parts: the cardo, the stipes with a single lobe, and the maxillary palp. The cardo and stipes lie in the membraneous area below the foramen magnum and alongside the postmentum. The cardo is an elongate, sinuate sclerite fused ventrally to the triangular stipes. Of the two endite lobes of the primitive coxopodite, one has been lost in Diptera. Most early workers assumed the maxillary stylet in this and other groups of Diptera to be the galea. More recently, however, this has been shown to be in error; it is the lacinia that is present and the galea which has been lost (Matsuda, 1965). Distally the lacinia possesses a number of backwardly directed teeth which are referred to in the species descriptions as "maxillary teeth." The maxillary palp consists of five segments, the third being swollen and possessing a large sensory organ, the inner surface of which is generally lined with spatulate sensilla (Fig. 4). The males have the lacinia reduced, with a fringe of distal hairs rather than teeth. Likewise, the maxillary palp of the males has the third segment considerably smaller and less swollen but still with a small, deep sensory organ often containing a few spatulate sensilla (Fig. 34).

The labium of *Culicoides* consists of a postmentum, prementum and the two-segmented palpus. The postmentum is a long, tapering sclerite lying medially in a membraneous field below the foramen magnum. The prementum is broad and narrower posteriorly than the broad, blunt anterior end. As in other Nematocera, the ligula has been lost and the palpi are represented by the two-segmented labellum.

In females the hypopharynx is a blade-like structure with a median salivary duct and bearing a number of apical teeth. According to Gad, the salivary canal opens in the proximal half or third of the stylet. The hypo-

pharynx is proximally incorporated into the cibarial pump. In males the hypopharynx is shorter and, like the other mouthparts, lacks teeth but possesses a few bristles.

Thorax

The thorax is dorsally convex and extends anteriorly so as to cover the posterior region of the head slightly. The most conspicuous aspect of its anterior end is a pair of humeral pits, which lie at the anterior margins of the humeri. A pair of rather indistinct lines, the pseudosutural foveae, project caudally to near the lateral margins of the scutellum. The posterior portion of the mesonotum is more or less flattened and possesses a pair of submedian areas reputed to be sensory structures. The scutellum is transverse and in most species possesses two types of setae. The larger setae, designated here scutellar macrosetae, are usually arranged so that there is a median and a lateral pair. The smaller setae, the scutellar microsetae, generally occur in a specific pattern more or less characteristic for a species. The postscutellum is arched and bare.

The legs of *Selfia,* as in other *Culicoides,* are slender; however, the femora may be slightly expanded. The legs are devoid of modified spines or scales such as are found in other genera. The apex of the fore tibia bears a spur and a tuft of modified hairs, while the hind tibia possess a spur and two rows of spines; the more distal row contains four or five stout spines, while the second is a much weaker row. The basal four tarsomeres of the fore and hind legs of each species, except *brookmani,* have a stiff distal spine (Fig. 64), while the tarsomeres of the middle legs have two. The basitarsus is at least twice as long as the second, and the fourth is always shorter than the fifth. The only example of sexual dimorphism in the legs is the pretarsal claws. In the females they are simple structures (Figs. 34-35), but in the males they have a bifed apex (Fig. 6).

The posterior surface of the trochanter and anterior surface of the basal end of the femur contain dense fields of campaniform sensilla. These are present in both sexes.

There are two types of hairs on the wings: very short microtrichia, which are of uniform density over the entire wing, and longer macrotrichia, whose density and size varies. The wings of the species of this subgenus lack the pattern of spots characteristic of most groups of *Culicoides,* formed by varying densities of microtrichia.

The veins of the wing are much stronger at the anterior edge, the costa, radius and M_{1+2} being stout, whereas the more posterior ones are much less so. There are two well-developed radial cells, the distal cell being broader than the more slit-like proximal one. The nomenclature of the wing veins follows the Tillyard modification of the Comstock-Needham system, in

which the anterior branches are M_1 and M_2 and the posterior branches M_{3+4} and Cu_1. There are two short, incomplete veins lying at the anterior margin of the vannal cell, the Cu_2 and 1st V.

The wings of the males are generally shorter, more narrow, the radial cells less well developed, and the denser covering of macrotrichia usually found in females is generally lacking. The measurements of wing length is made from the basal arculus to the wing tip.

Abdomen

The female abdomen is broad, tapering posteriorly, the sclerotized sternal plates small except for those of segments 7-9, and the pleural membrane extensive so as to allow for engorgement. On both the tergal and sternal plates there are several areas which show up as "clear" spots under phase contrast microscopy. Close examination reveals that on the tergum there is a single pair of these spots lying in the unpigmented (unsclerotized?) region of the first segment and two pairs in the sclerotized tergal plates of segments 2-8 (Fig. 7). At least in *C. tenuistylus* there are clear areas also around the tergal setae. The first six sterna are not as well sclerotized as the terga, but the clear areas are nonetheless present. The condition in the more sclerotized seventh and eighth sterna closely approximates that of the tergal plates. These clear areas are devoid of microtrichia which normally densely clothe the plates. The function of these areas, which occur in both sexes and in the genus *Stilobezzia* (Das Gupta and Wirth, 1968), is at present unknown.

The posterior abdominal sterna of the female are much more heavily sclerotized than the anterior ones, apparently to give rigidity to this region during oviposition. The sternum of the eighth segment has a median posterior excavation, the depth of which varies with species. The posterolateral margins of the excavation are sometimes modified into laterally directed, hook-like processes (Fig. 221). The sternum of the ninth segment is modified into a pair of mesally projecting but separate structures. The mesal ends are swollen and in some species there is an anteriorly projecting, thumb-like lobe which serves to support the opening of the bursa (Fig. 123). The venter of the ninth segment has been referred to as the "subgenital plate" by Pomerantzev (1932). Lying in the membrane between the median excavation of the eighth sternum and the divided portion of the ninth is the triangular opening of the oviduct, bordered by setae.

The tenth segment is small and bears the rather large oval cerci. Between the tergum and sternum of this segment is the anus. Pomerantzev has termed the tenth segment the "pre-anal cone."

The internal reproductive organs of the females and the external genitalia of the males make *Selfia* distinct from all other groups of *Culicoides*. The three spermathecae of the females are very elongate and

digitiform, often extending as far forward as the sixth segment. They range from lightly sclerotized but still discernible under phase contrast microscopy, as in *multipunctatus,* to virtually unsclerotized, as in *brookmani.* The three spermathecae are equal in *multipunctatus,* while five of the remaining six species have two of them very long and one shorter. In addition, those of *multipunctatus* possess slightly enlarged basal chambers, while the apices are slightly contracted and parallel-sided. Each spermatheca is connected to the bursa by a minute duct.

The bursa is a long, broad structure in *Selfia,* ranging in length from 60-70μ and with a large posterior opening in all species except *multipunctatus. Culicoides multipunctatus,* to my knowledge, differs from all other species of *Culicoides* in having three separate ducts within the bursa. Although there are three separate openings to the bursa, I have been able to trace the separate ducts only to about three-fourths of the length of the bursa (Fig. 26). At this point it becomes very difficult to ascertain whether they continue separately into each of the spermathecae or coalesce into a single tube. As will become evident later, the openings correspond to the trifid male aedeagus.

The male genitalia likewise exhibit a number of peculiar modifications. They arise from the ninth segment and, if we can extrapolate from recent embryological findings in other closely related groups of Nematocera, are of sternal rather than appendicular origin. The ninth segment is a scleroma consisting of the fused tergum and sternum, easily seen in a lateral view of the genitalia of, for example, *hieroglyphicus* (Fig. 9). The ninth sternum is variously modified in males of *Selfia.* In *tenuistylus* its posterior margin is straight and lacks any apparent modification, while in *multipunctatus* and *brookmani* it is posteriorly emarginate. In *jamesi* and *jacksoni* n. sp., there is dimorphism within a number of populations with respect to this structure. The ninth sternum in these two species may be emarginate or may have a deep but very narrow cleft (Figs. 216, 220) that almost bisects the venter of the segment. One specimen of *jamesi* from Garfield County, Utah, has a straight, unmodified sternal margin, as in *tenuistylus,* providing in a single species an entire spectrum of sternal modification from the straight, unmodified edge through the emarginate form to the deep cleft.

A third type of sternum, found in *hieroglyphicus* and *denningi,* has a pair of contiguous, posteriorly projecting mesal lobes. In *hieroglyphicus* the lobes are greatly extended, and the line separating the lobes continues anteriorly and completely divides the venter of the segment.

The ninth tergum is a posteriorly tapering structure with divergent apicolateral processes and a number of long setae on the dorsal surface. The principal changes in the ninth tergum involve the shape of the posterior margin and the length and shape of the apicolateral processes.

The lateral genital claspers, or parameres, are composed of two parts: the broader, proximal basimere and the tapering, distal telomere. The reasons for use of these terms for the lateral claspers and claspettes for the internal sclerotized rods have been adequately discussed elsewhere (Atchley, 1967, 1969).

The basimere is oblong, generally with a moderately dense covering of long setae. Its inner anterior corner is sclerotized more heavily than the remainder, and sometimes, as in *hieroglyphicus* or *denningi,* a sclerotized shelf or knob is formed across its cephalic end to serve as a point of articulation for the aedeagal arms. In *hieroglyphicus* and *denningi,* there is a small lateral swelling on the arm which articulates with the basimere. The basimeric root is primarily single and in *hieroglyphicus, denningi* and *brookmani* lacks any processes. There is a small, slightly curved projection on the posterior surface of the root in the remaining species. In all *Selfia* species the basimeric root articulates with the fused claspettes.

The function of the small posterior process of the root is uncertain. In *multipunctatus* it appears to rest on the posterior shoulders of the claspettes, and in some specimens a sinuate area on the process appears to correspond to a similar surface on the posterior edge of the claspettes. In *tenuistylus* there is a globular process arising from the depression created by the posterior projection bearing numerous fine, mesally directed projections (Fig. 200). A rugose membrane arises from the region of the posterior process in *jamesi* and apparently attaches to the aedeagus. The aedeagus in this species is somewhat longer than in other species and the membrane may assist in holding it in place.

The telomere is basally stout in all species and is tapered distally. The apex may be variously modified. In *tenuistylus* and *multipunctatus* it is unmodified, while in *brookmani* there is a slightly recurved subterminal spine. In the other species there is an increasing trend toward expansion into a foot-shaped apex culminating in the condition exhibited by *jamesi.*

The claspettes have become fused, but in varying degrees. In *multipunctatus* the claspettes, although fused, most closely approach the divided condition of most other groups in that the arms are quite long and consolidated only in subhemispherical shape. Further evidence of proximity to the divided condition can be found in the divided median posterior process which, for example, has become completely fused in *brookmani.* The degree of fusion of the claspettes is greater in the other forms with a corresponding trend toward prolongation of the median posterior process.

The aedeagus is the structure exhibiting the most marked divergence in this subgenus. In *multipunctatus* it is distally trifid with the median prong longer than the faintly divergent lateral pieces. Critical examination of the apex under oil immersion by phase contrast microscopy reveals a very fine,

pale band traversing each prong (Figs. 22-23). These bands originate at the posterior end of the aedeagal arch as a simple duct, which then branches into three, one in each prong. The pale bands in the lateral prongs are larger and much more distinct than in the median one; however, examination of a number of specimens confirms the presence of one in the median prong. In a few specimens a terminal opening could be seen in the median prong. These ducts are more easily seen in reared material than in light trap specimens, apparently due to the fact that the former specimens have not had as long to harden. They appear to be the sperm ducts as evidenced by the shape of the bursa of the females.

There is only a single reference in the literature dealing with sperm transfer in *Culicoides* and this concerns *C. nubeculosus* (Pomerantzev, 1932), one of the more advanced species of this genus. Sperm transfer in this species, which has a large, broad aedeagus, is accomplished by spermatophores. The shape of the bursa in *multipunctatus,* with its three separate openings, coupled with what would appear to be three fine sperm ducts in the aedeagus, strongly suggests that *multipunctatus* utilizes liquid semen rather than spermatophores for sperm transfer.

In four species, there exists a modification of the aedeagus which is, to my knowledge, unique in the entire genus. This is an eversible aedeagus, found in *denningi, hieroglyphicus, tenuistylus* and *jacksoni.* Here the aedeagus is eversible and composed of two rigid, heavily sclerotized, aedeagal arms and a rather pliable median structure which is capable of being everted to varying degrees. In *jacksoni* it can be everted to roughly one-third to one-half the length of the arms.

In *hieroglyphicus* and *denningi* there is a pair of indistinct rod-like sclerites on the posteromesal margins of the aedeagal arms which may correspond to the lateral edges of the eversible median portion. These sclerotizations are most easily seen in the uneverted condition (Fig. 119) and become progressively less distinct as the aedeagus is everted (Fig. 118). Specimens exhibiting the maximum degree of eversion have very indistinct sclerites which have moved posteriorly. In specimens cleared in phenol, a thick-walled duct is evident which originates from the accessory gland in the region of the sixth to eighth abdominal segments and attaches to the anterior end of the aedeagus. This gland may serve as a sperm pump.

In *tenuistylus* and *jacksoni* the aedeagus is longer, thicker and capable of being everted to a greater degree than in *hieroglyphicus* and *denningi.* Both *tenuistylus* and *jacksoni* have a horizontal bar-like connection between the aedeagal arms, which possesses a median opening. In several phenol-cleared specimens of *jacksoni* the prominent ejaculatory duct can be seen connecting the median posterior opening of the aedeagus with the accessory gland in the segments 6-8. These structures superficially resemble those described by

Pomerantzev for *C. nubeculosus*. In some similarly prepared specimens of *hieroglyphicus*, the vas deferens can be seen running posteriorly along the surface of the accessory gland before turning back anteriorly to unite with the testes. The accessory gland of *hieroglyphicus, denningi, tenuistylus* and *jacksoni* is heavily musculated and readily visible in phenol-cleared material.

The aedeagus of *C. jamesi* is quite elongate and apparently a permanently everted structure. There is a trough-like median process which extends anteriorly between the aedeagal arms for some distance (Fig. 219). It is possible that the lateral sclerotized margins of the trough represent the modified rod-like sclerites of the eversible aedeagus of *hieroglyphicus* and *denningi* which have become fixed in their present position. The long, stout aedeagal arms of *jamesi* apparently give some degree of rigidity to the aedeagus.

It is difficult to see exactly where the ejaculatory duct terminates in the aedeagus of *jamesi*. In some specimens it would appear to end at the anterior end of the aedeagus, while in others it extends more posteriorly. The elucidation of the ejaculatory duct's connection will probably require histological preparations.

The remaining species, *brookmani*, possesses a very peculiar aedeagus. This species has unusual, boomerang-shaped aedeagal arms. The median posterior portion is more or less triangular, with stiff lateral margins and a slightly recurved apex. The median portion is very thin and apparently not capable of any kind of everting action, although there is some variation in length of the part apical to the lateral sclerotizations. In addition, the median process in a number of specimens is ventrally concave, and in at least two good preparations there appears to be a fine membrane extending from the tips of the boomerang-shaped aedeagal arms to the tip of the median process. All of these conditions, i.e., the membrane, the concave median process, the aedeagal arms and the fused claspettes, produce a pocket or cavity in the genitalia, best seen from lateral view.

The ejaculatory duct of *brookmani* is considerably larger and with much more heavily musculated walls than in the other species of *Selfia*. At its narrowest point, where it opens at the mesal corners of the aedeagal arms, it is 26-30μ wide. Great quantities of sperm can often be seen in the ejaculatory duct. The peculiar shape of the pocket formed by the fused claspettes and aedeagus, the very broad, ejaculatory duct and the large bursa in the females would tend rather strongly to suggest that *brookmani* utilizes spermatophores for sperm transfer.

If these hypotheses regarding the use of liquid semen by *multipunctatus* and spermatophores in *brookmani* can be substantiated, this would indicate a marked difference in the mechanism of copulation between these two

closely related species. *Culicoides multipunctatus* would probably require a considerable amount of time to complete copulation, and this would no doubt occur on some substrate. *Culicoides brookmani,* however, might be capable of mating in a much shorter time simply by the exchange of a spermatophore.

There is an interesting correspondence in *Selfia* between the size and shape of the male aedeagus and the type of spermathcae in the females. Both *multipunctatus* and *brookmani* have a rather small, short aedeagus and correspondingly small spermathecae. The remaining species have a larger, longer aedeagus, either by elongation or eversibility, and the spermathecae are much longer.

The tenth segment of the males is an indistinct and membranous bearing the anus and a pair of small setigerous cerci and is continuous with the membrane of the ninth tergum.

Pupa

The pupae of *Culicoides* superficially resemble those of many other groups of Nematocera. There are three principle body regions: the small head, a compact, rigid thorax, with a characteristic hump in the region of the mesothorax, and the more elongate, flexible abdomen. Each body region possesses numerous tubercles bearing spines of varying sizes and shapes. The only obvious examples of sexual dimorphism are found in the last abdominal segment and the width of the operculum. The only readily discernible difference between the pupae of *Selfia* and those of other groups of *Culicoides* is the number of dorsolateral bristles.

Head

The head is easily delimited, particularly from a lateral view. The conspicuous antenna originates on the lateral region, curves down over the eyes and terminates between the tibia of the mesothoracic leg and the anterior edge of the wing. Lying between the antennae are the eyes which are outwardly evidenced by a pattern on the pupal cuticle. The dorsal part of the head is occupied by the large operculum whose lateral margins are the arms of the ecdysial suture. The operculum is clothed by a large number of anteriorly directed denticulations. Lawson (1951) has shown the operculum to be the pupal frontoclypeus, but the term operculum is worth retaining on a functional basis since it describes the role of this sclerite. At the time of adult emergence, the ecdysial split begins at each side in an area below the *am* tubercles, then proceeds dorsally until the suture arms unite to become a median dorsal split. The operculum thus does not separate completely but is retained as a hinged flap.

At the anterior margin of the operculum is a pair of prominent protuberances, the *anteromarginal (am)* tubercles, each of which possesses a large, stout spine. Immediately posterior to these tubercles is a minute, clear spore in which, upon close scrutiny, can be seen a fine hair.

Another prominent tubercle occurring just lateral to the operculum and posterior to the *am* tubercle is the *antero-dorsal (ad)*. The latter bears a large spine and a smaller one.

On the ventral side of the head just below the region of the eyes are two pairs of setae, the more lateral pair the *ventro-lateral (vl)* setae, the median pair, which arises from the region just over the adult proboscis, the *ventro-median (vm)*.

Thorax

The thoracic region of the pupa gives rise to the conspicuous respiratory horns and the sheaths of the wings and legs. In six of the seven species of *Selfia* these horns are elongate structures, each containing a single trachea with four to nine apical spiracular openings and two to four lateral openings. The latter generally open on protuberances. There are a number of folds in the cuticle, usually most prominent above the distalmost lateral spiracular opening, referred to as lateral convolutions.

The respiratory horn of *Culicoides brookmani* is strikingly modified into a large triangular structure containing numerous small tubules. It is very broad apically and tapering proximally and has two distinct groups of respiratory openings (Fig. 65). One group is found at the apices of the basal tubules, while the other is located along the mesal J-shaped trachea. Of the latter group, those on the vertical axes of the trachea open dorsally, those on the horizontal axis open ventrally.

Because of the anterior position of the horn on the thorax, most authors have erroneously construed it to be of prothoracic rather than mesothoracic origin. Lawson (1951) stated that the prothorax can be delimited by a transverse furrow immediately anterior to the hump. He suggested a prothoracic origin of the horn on the basis of the tracheal attachment and states that "the spiracular chamber arises from the prothorax of the adult . . ." and further ". . . this (ring of sclerotization) must be the rudiment of the prothoracic spiracle of the adult." Lawson interpreted the anteriormost thoracic spiracle, which often lies in the mebrane between the pro- and mesothoracic segments, as prothoracic in origin, but morphologists consider it mesothoracic (Snodgrass, 1935).

Beside the respiratory horn and slightly dorsad from the antenna is a small tubercle, the *dorso-lateral (dl)*, which possesses a long filamentous seta and a short stouter one. Lawson indicated that *C. nubeculosus* had only two *dl* spines, but Jones (1961a) found that in the North American species

of *Culicoides* only those of the subgenus *Selfia* had two spines, all others having three.

Posterior to the respiratory horn and beside the ecdysial cleavage line are five *dorsal (d)* tubercles. Tubercles d_1 and d_2 are more anterior and stout than the others, while d_3 is the most posterior tubercle and has a short spine. Tubercle d_4 generally lies just laterad from d_2 and d_3 and has a long, filamentous seta, while d_5 is represented by a pore (=sensilla of Lawson) and lacks a spine or seta. The cuticle around the *dorsal* tubercles may be either patterned or relatively smooth, depending on the species.

The mesonotum is well demarcated as the region possessing the large pad-like wing sheathes, while the metanotum can be distinguished not only by a suture separating the two thoracic regions but also by the sheathes of the halteres.

Abdomen

The abdominal segments are in longitudinal alignment with the thorax and are relatively motile, although not to the extent seen in mosquitoes or chironomids. The first segment is smaller and not as distinct as the remainder, since it is somewhat obscured by the pads of the thoracic appendages.

The abdominal segments possess a large number of tubercles, which are generally prominent, most bearing posteriorly projecting, spine-like setae, and have their lateral corners often extended into spiniform processes. The term "spiniform" is used in a rather broad sense to describe the spine-like projection of the lateral margins of some tubercles. Some authors have referred to this as a "spined" condition; however, in tubercles that lack a seta, the use of the term "spined" for the projection of these lateral margins can become confusing. The tubercles may have "spiniform," "semi-spiniform" or "rounded" posterior margins (Figs. 101, 235). If the projection of these lateral margins terminate in a point, the tubercle was considered to be "spiniform," but if the projections were rounded, they were scored as "semi-spiniform." The "rounded" condition refers to those forms where there is no extension of lateral corners, but rather the apex is truncate or rounded off. The tubercles of the first and second segments are reduced and are represented by setae only. Likewise, on the eighth segment some are completely lacking and not even setae are present. The ninth segment (anal segment, according to some authors) is devoid of tubercles or setae.

There are usually five complete series of tubercles on abdominal segments 3-7. Following Jones (1961), their numbering begins with the center pair ventrally and proceeds laterally in each direction, ending with the center dorsal pair.

On the dorsal side of the abdomen along the posterior margin of a segment are five pairs of tubercles, the *dorsal posteromarginals (dpm)*. In

Selfia only pairs 1, 2 and 5 possess spines; 3 and 4 have a socket but no spine. On the lateral surface along the posterior edge of the segment are the three pairs of *lateral posteromarginal (lpm)* tubercles, while on ventral posterior margin are the three pairs of *ventral posteromarginals (vpm)*. The other two sets are submarginal at the anterior end of the segment and include two pairs of *dorsal anterosubmarginals (dasm)* and a pair of *lateral anterosubmarginals (lasm)*.

The ninth segment possesses an anterior border of spicules and a pair of tapering, strongly divergent, lateral projections. The latter are darkly pigmented on the apical third or half. Male pupae can be quickly distinguished from females by the presence of the genital lobes on the ventral side of the ninth segment. These lobes are the sheaths of the genital appendages of the male (basimere and telomere), and often the specific identity of live pupae can be determined on the basis of these structures. Lying between the bases of the genital lobes in some species is a small swelling often bearing a posterior protuberance. This swelling is lacking in the males of *multipunctatus* and *brookmani* and the females of all species. Snodgrass (1959) illustrates a similar structure in mosquito pupae of both sexes and refers to it as the tenth segment.

Larva

Larvae of *Culicoides* are elongate and cylindrical with a well-sclerotized head capsule. The second abdominal segment is generally largest in diameter, the body tapering slightly in both directions. In addition to the head capsule, there are three thoracic and nine abdominal segments. Except for a prothoracic pseudopod present only in the first instar, the body lacks appendages.

The head capsule of *Selfia* resembles that of other *Culicoides* in being composed of two sclerites. The first is the dorsal sclerite, according to Lawson the frontoclypeus, bounded laterally and posteriorly by the U-shaped ecdysial or epicranial suture, which originates anterior to the postoccipital ridge and extends to near the antennae. The other is of complex origin, comprises the lateral and ventral walls of the head, and is delimited from the postoccipital ridge or collar by the postoccipital suture. There is some difference of opinion as to whether the postoccipital ridge would be considered a true head sclerite, that is, whether the postoccipital suture is actually an intersegmental line or simply a secondary suture. Kettle and Lawson (1952) consider the postoccipital ridge to be a head sclerite, while Lawson (1951) and Linley and Kettle (1964) refer to it only as a head region.

The foramen magnum is almost completely surrounded by the narrow collar-like postoccipital ridge, except for a small gap immediately posterior to the epicranial suture. Lawson has shown that several muscles of the head

and prothorax attach on this ridge. At the anterior end of the head capsule is a second band, the subgenal band, which forms an articulating surface for the mouthparts.

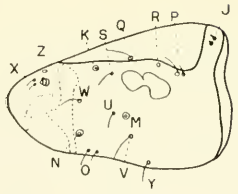
The small antennae lie anterior to the subgenal band and apparently are four segmented, although, due to their minute size, few morphological details can be gleaned from them.

The eyes are strongly pigmented and are usually on the lateral walls outside the epicranial suture; occasionally, however, they are more dorsal and the suture passes through them. The eyes possess only a single simple lens.

The mandibles are well sclerotized and with an apical, slightly curved, sharp hook and a small thumb-like process appressed to the inner margin. The basal portion is stout, with a small external seta.

The dimensions of the larval head are generally expressed by three measurements and a ratio. These include the *head length,* which is measured along the mid-dorsal line from the anterior margin of the labrum to the posterior edge of the postoccipital ridge. The *head width* is obtained by measuring the head at its broadest point, usually at about a third of the length from the posterior end. The *width of the oral ring* is taken at the hind border of the subgenal band. The *head ratio* is obtained by dividing the length by the width.

The primary internal sclerotized structure of the head capsule is the two-part pharyngeal skeleton (Fig. 14). The ventral hypopharynx is rather elongate, becoming trough-like posteriorly and bearing a fringe of fine hairs on its posterior margin. The salivary glands open at its membranous anterior end. The epipharynx is suspended in the dorsal trough of the hypopharynx by its well sclerotized arms. It consists of two long, lateral arms and a massive median portion which possesses several combs with a number of posteriorly directed teeth. In certain groups of *Culicoides* there may be as many as four combs; however, in the five species of *Selfia* examined, there are only two combs. Ventral to the bases of the lateral arms of the epipharynx are three sclerites, the dorsal combs, each with a posterior row of sharp teeth, and the frontal comb. The latter is anterior to the dorsal comb; in *hieroglyphicus* and *denningi* it has 5-7 large, rounded teeth, while in *jamesi* and *jacksoni* the teeth are smaller, sharp and more numerous. The term "frontal comb" is used here since the homology between this structure and the combs 2-4 of Kettle and Lawson is not at all clear. Linley and Kettle (1964) have referred to this comb as the fourth in *C. hoffmani,* a species which also has only two combs. In illustrations of the epipharynx of the species of *Selfia,* the frontal comb is often drawn with the teeth projecting anteriorly rather than posteriorly. This could be due to mounting technique, that is, flattening of the epipharynx when dissected out of the



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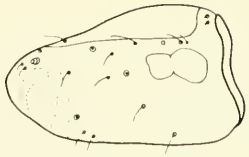

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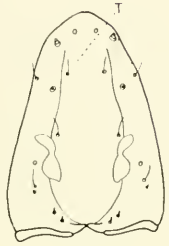

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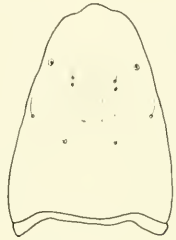

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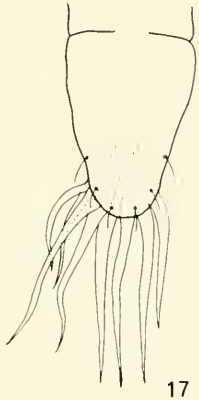

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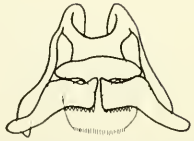

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16

FIGS. **10, 12, 13.** Lateral, dorsal and ventral view of larval head of *C. denningi*. FIG. **11.** Lateral view of larval head of *C. tenuistylus*. FIGS. **14-16.** Dorsal and lateral views of epipharynx and hypopharynx of *C. denningi*. FIG. **17.** Anal papillae of *C. denningi* larva.

head and mounted. Certain *in situ* preparations would tend to support this assumption. Figure 14 shows a dorsal view of the entire pharyngeal skeleton. Figures 15 and 16 give some idea of the position of the epipharynx in the trough of the hypopharynx.

Kettle and Lawson have described two types of pharyngeal skeleton in the British species of *Culicoides*. The *C. nubeculosus* group has a massive median portion with strong teeth on the dorsal comb. Their function appears to be grinding and crushing. The hypopharynx is strongly sclerotized and pigmented.

In the second type the degree of sclerotization and pigmentation is considerably less, the trough of the hypopharynx being mostly membranous. The strong plates of the median portion of the epipharynx of the first group have become modified into combs with posterior teeth, apparently for sucking and sieving.

The *Selfia* species would be difficult to place in such a scheme because there are only two sets of epipharyngeal combs and the epipharynx has no additional median sclerites as in *nubeculosus*. The degree of sclerotization and pigmentation of the hypopharynx is less than in *nubeculosus* but considerably more than what Kettle and Lawson depict for *C. albicans*, a member of their second group.

The chaetotaxy of the head capsule of only two species of *Selfia, denningi* and *tenuistylus*, could be studied since most of the larval material used in this study consisted of associated exuviae, which are not well suited for chaetotaxal studies.

The number of setae on the head capsule of *Selfia* species corresponds closely to that occurring on other species of *Culicoides*, although there is some variation in their position and size and in presence or absence of certain pits. The setae and pits are arranged as follows (Fig. 10). On the dorsal surface generally just behind the posterior curvature of the epicranial arms are the *j* pits which contain two pairs of conical processes. Above the posterodorsal corner of the eye and below the epicranial suture are the two *p* setae, the anterior one being larger. The frontoclypeus bears a pair of *t* setae at the anterior end and of *q* setae at about midlength. In *tenuistylus* the *q* setae lie on the lateral walls just below the epicranial suture. Between the *q* and *p* setae and just above the eye is the *r* pit. Anterior to the eye and below the epicranial suture are the *k* pit and the *s* seta, the latter lying between the eye and the *k* pit. On the lateral wall immediately posterior to the subgenal band is the *w* seta and ventrad to *w* but still just behind the band is the *n* pit. Below and slightly behind the *n* pit are the *o* setae. On a diagonal between the *y* and *t* setae lie the *u* and *v* setae. Posterior to the *u* seta and anterior to *v* lies the *m* pit. Just anterior to each antenna are the *x* setae, and just above it is the *z* pit.

Four interspecific differences in chaetotaxy were noted between *denningi* and *tenuistylus*. In *denningi* (Figs. 10, 12-13) seta *q* lies at the lateral margin of the frontoclypeus, while in *tenuistylus* (Fig. 11) it is on the lateral wall just below the epicranial suture. Seta *u* and pit *m* in *denningi* lie some distance below the anteroventral corner of the eye, but in *tenuistylus* they are in front of and on the same level as the eye. Finally, the *p* setae of *denningi* are slightly behind the posterodorsal corner of the eye; however, in *tenuistylus* they are above the posterior half of the eye.

The chaetotaxy of only four other North American species have been described in enough detail to allow comparison. These include *C. tristriatulus* (Williams, 1951) *C. mellus* and *C. furens* (Wirth, 1952b) and *C. furens* and *C. hoffmani* (Linley and Kettle, 1964). The species of *Selfia* differ from *tristriatulus* in the very unequal size of the *p* setae, the spatial relationship of the *p* setae and *r* pit to the eye, the proximity of the *u* seta to pit *m* in both *Selfia* species. In addition, *tenuistylus* differs in the more dorsal position of *u* and *m* together with the position of *q*. With the possible exception of *hoffmani, tenuistylus* differs markedly from all other North American species in the position of *u* and *m*. It differs even from *hoffmani* in these characters, although not to as marked a degree as in other species.

The two *Selfia* species can be distinguished from *C. mellus* by their having two *j* setae. They can be distinguished from *hoffmani* by the presence of two conical processes arising from the *j* pits, the presence of a *z* pit and the relationship between the *w* and *u* setae. They differ from *furens* by the unequal size of the *p* setae.

The anal papillae were examined in *denningi* and found to be eight in number and either extruded from the anus or retracted (Fig. 17). They are broad basally, tapering to a fine apex, and are about 140μ long. The anal setae consists of three pairs of medium sized setae. There are no perianal bristles as found in *C. hoffmani*.

SYSTEMATICS

Introduction

The subgenus *Selfia* was erected by Khalaf in 1954 to include five nearctic species: *brookmani* Wirth, *hieroglyphicus* Malloch, *jamesi* Fox, *multipunctatus* Malloch, and *tenuistylus* Wirth, and Fox (1955) added *denningi* Foote and Pratt. These six species and *jacksoni,* described here as new, constitute the known species of *Selfia* which, zoogeographically speaking, is restricted to the Nearctic region.

Three infrasubgeneric complexes are recognized which represent separate phyletic lineages. These groups, the *multipunctatus, hieroglyphicus* and *jacksoni* complexes, can be distinguished on the basis of morphology of the

male genitalia, pupae and, in the case of the *hieroglyphicus* and *jacksoni* complexes, the larvae. Larvae are unknown in the *multipunctatus* complex.

Any attempt to ascertain the nearest relatives of *Selfia* is hampered by inadequate knowledge of the subgeneric groupings in the remainder of the genus. There has been only one attempt at delineating phylogenies within the genus *Culicoides* (Khalaf, 1954) which, in my opinion, is ambiguous and often inaccurate. For instance, Khalaf stated that "the group *(Selfia)* stands distinctly in a unique position in this group," but earlier had opined that *Selfia* should be considered as "intermediate" between the *Monoculicoides* and *Culicoides* s.s. groups and *Oecacta*. He further stated that unless many species are considered to be extinct, *Selfia* cannot be regarded as monophyletic. This assumption is totally without foundation. A thorough criticism of Khalaf's paper is beyond the scope of this paper; consequently, only passing reference will be made to it in the succeeding discussion.

The bizarre modifications of the reproductive systems of both sexes indicate an early divergence from the main line of evolution in *Culicoides*. Within *Selfia, multipunctatus* appears to have retained a number of pleisiomorphous character states, such as the only partially fused claspettes, unmodified telomere, three equal and relatively well-sclerotized spermathecae, etc., and could be considered the most primitive extant number of the subgenus.

In several respects *multipunctatus* exhibits considerable resemblance to *C. sejfadinei,* a species found in the Old World. The rather close similarity between *multipunctatus* and *sejfadinei* with regard to the structure and number of spermathecae, the basimeric root and various other structures, indicates that *multipunctatus* was probably derived from some species closely related to *sejfadinei*. Further, this latter species possesses unmodified, rod-like claspettes, not very different from those of *multipunctatus*. The condition of the claspettes in *sejfadinei* is, in my opinion, the pleisiomorphous state of this character and not the fused condition, as Khalaf would have us believe.

Apparently the first of the remaining complexes to split off from the *multipunctatus* complex was the *hieroglyphicus* line, composed of *hieroglyphicus* and *denningi*. Within this group the more simple nature of the ninth sternum, telomere apex and spiniform condition of most of the *lpm* tubercles in the pupae would indicate *denningi* to be the more primitive species.

The remaining group, the *jacksoni* complex, including *jacksoni, tenuistylus* and *jamesi,* was probably derived from the *hieroglyphicus* rather than the *multipunctatus* complex, as evidenced by the common possession in the *hieroglyphicus* and *jacksoni* complexes of a peculiar apomorphous structure, the eversible aedeagus. This structure, which is small and apparently not

very well developed in the *hieroglyphicus* line, is quite pronounced in *jacksoni* and *tenuistylus*. In *jamesi* the aedeagus has lost its eversible nature and the median "permanently everted" posterior portion has become an elongate, trough-like structure. This represents a still more apomorphous condition than the other two *jacksoni* species.

Of the seven species of *Selfia*, the placement of *brookmani* into a phylogenetic scheme is not without some difficulty. This species possesses a number of structures not found in any of the other species of this subgenus, including the very peculiar pupal respiratory horn, aedeagal complex and the apparent use of spermatophores to transfer sperm. I have tentatively placed *brookmani* in the *multipunctatus* group with the assumption that if, in fact, it was derived from *multipunctatus* or some similar but now extinct form, it has undergone rapid evolution to achieve its now somewhat unusual morphological and biological attributes.

Relationships among *Culicoides* and other closely related genera of ceratopogonids have not been worked out due to the lack of critical taxonomic studies in all genera and the absence of detailed studies on the morphology and systematics of the more primitive groups of *Culicoides*.

The recent extensive revision of the oriental species of *Stilobezzia* by Das Gupta and Wirth (1968) and the description of several quite generalized species of Asian *Culicoides*, together with this account of the morphology and taxonomy of *Selfia*, disclose a number of heretofore unrecognized similarities between *Stilobezzia* and the more primitive species of *Culicoides*. I am indebted to Dr. Willis W. Wirth in this brief discussion for his helpful comments on various aspects of ceratopogonid phylogeny.

At first glance *Stilobezzia* might appear to be quite distinct from *Culicoides* due to the modification of the radial cells of the wing, heavily spined tarsomeres, shape of the pre-tarsal claws, etc. Comparison of certain structures of the genitalia, however, may belie this seemingly marked divergence in other features. The very simple shape of the claspettes in *C. sejfadnei* is quite similar to a number of species of *Stilobezzia*. The simple rod-like aedeagal arms in the *hieroglyphicus* complex are much like those in such *Stilobezzia* species as *antennalis* and *diversa*, while the aedeagal collar of *multipunctatus* resembles a similar structure in certain *Stilobezzia* species. The shape of the eighth and ninth sternum in *hieroglyphicus* females is virtually identical with that in the *Poikiloptera* group of *Stilobezzia*.

With respect to the biology of the two genera, the insectivorous behavior as found in *Stilobezzia* likewise occurs in the *anophelis* group of the subgenus *Trithecoides*, a primitive group of Old World *Culicoides*.

Statistical Methods

The major emphasis of this paper is not the phylogeny of *Selfia*, but rather a critical analysis of phenetic variation. This will involve, first, an

assessment of geographic variation in *hieroglyphicus, denningi* and *jamesi* and, secondly, an analysis of natural hybridization among these three forms.

Studies of geographic variation are of importance not only because of their obvious contribution to the taxonomy of the group, but also because they may bring new light to bear on the adaptative significance of morphological variation, rates and direction of gene flow, the nature of possible selective agents and past distributions.

The availability of a multiplicity of groups, each contining a number of individuals, gives rise to two sources of variation. One of these, the within group variance-covariance matrix, indicates dispersion within the various groups; the other, the between group variance-covariance matrix, indicates the dispersion between the groups. There are several multivariate techniques which utilize one or the other source of variation, two of which, generalized discriminant functions (=canonical variates; Seal, 1964) and principal components, were employed in this study.

Discriminant functions are the principal axes of a between-group matrix after standardization by the within group matrix. This standardization, first of all, adjusts each measurement by the variance of every other measurement and, thereby, alleviates the emphasis on factors such as age and size in the discrimination between groups and, secondly, maximizes the intergroup differentiation with respect to intragroup differentiation. For each of these principal axes there are coefficients *(K)* of the discriminant functions so that $K_1\overline{Y}_1+K_2\overline{Y}_2 \ldots +K_n\overline{Y}_n=P$, where $K_1 \ldots K_n$ are eigenvectors or direction cosines, $\overline{Y}_1 \ldots \overline{Y}_n$ are sample means and P is the point on the axis for a sample. Individual specimens can be plotted by substituting the individual character values $(\overline{Y}_1, \ldots, \overline{Y}_n)$ in place of the means. There is a characteristic root or eigenvalue for each axis which measures the dispersion of group means along the axis. Dividing a particular eigenvalue by the sum of all eigenvalues gives an estimate of the percent of the variation explained by that discriminant function. Chi square tests can be performed on each function and nonsignificant ones ignored. For a more detailed discussion of discriminant functions the reader is referred to works such as Seal (1964).

Sets of vectors were computed to show the change in the discriminant function that a character would generate if it varied independently. Character vectors were computed by dividing the coefficients of a given discriminant function by the standard deviation of each character obtained from the pooled within group variance-covariance matrix. When the vectors are compared with projections of means onto discriminant functions, trends in geographic variation become evident. In some cases, as in the leg or head measurements, the characters are strongly correlated; hence the vectors must be considered jointly rather than separately.

Variation is often depicted by bivariate scattergrams or three-dimensional models in which the positions of individuals or taxa can be plotted with respect to two or three characters. When a number of characters are employed, this procedure can become laborious and often is not very informative. Consequently, multivariate techniques such as discriminant functions or principal components are used to compress a large number of variables into fewer dimensions, which explain a great deal of the variation and can be projected into three-dimensional models. In this study, variation was analyzed in a small subset of adult characters and a larger set of adult and pupal attributes, the former by discriminant functions, the latter by principal components. The first three functions or factors, which account for the greatest proportion of the variation, were made the axes of the three-dimensional models. Sometimes, however, it is desirable to have an estimate of phenetic resemblance that takes into account all of the variation. A number of such estimates have been proposed (see Sokal and Sneath, 1963 for review). I have employed the principle of "generalized distance," developed by Mahalonobis (1936) and Rao (1948), as an additional estimate of phenetic similarity. This is a weighted coefficient in which both correlations among characters and variance of separate characters are considered. Generalized distance was originally used to study continuous variables that varied with the population and, therefore, had to take into consideration the mean and variance. This coefficient is generally not used by numerical taxonomists, since they are primarily concerned with discontinuous characters or coded continuous variables.

Generalized distance is defined by the expression

$$D^2=\beta_1 d_1+\beta_2 d_2+ \ldots +\beta_n d_n$$

where the β-coefficients are the weights of the characters in the discriminant function and d, the difference between mean values of each character in the two groups. In this paper the square root of D^2 has been taken; therefore, D is used. Those groups separated in a generalized distance matrix by a small value are more alike phenetically, with respect to the characters employed, than more widely separated pairs. The arrangement of groups of organisms connected by smallest value on a generalized distance matrix is generally referred to a *discriminatory topology*. In this study the means of each sample, after being projected onto the first three discriminant functions, were then connected by a straight line to that sample with which it shared the smallest value in the generalized distance matrix. In many cases, those samples which were closest together when the means were projectioned onto discriminant functions, are not the samples which share the smallest value in the generalized distance matrix. The reason for this is that the former considers only the first three components, which seldon explains all of the variance.

Since generalized discriminant functions consider all characters jointly, specimens with data missing for one or more characters must be excluded. This had a marked effect on the size of some samples, particularly those of *C. jamesi,* which were so small that they were deleted from the analysis. A further consequence of these small sample sizes was the omission of significance tests among localities for *jamesi.*

In some instances, however, samples with only a very few individuals were retained in the analyses. This was done when these specimens were from an unusual habitat or from a locality at a considerable distance from the remaining samples. Examples include the Fremont County, Wyoming, locality, which was a very warm, polluted stream, rather unusual for *denningi,* and the Meade County, Kansas, sample of *hieroglyphicus,* which was taken quite a distance from the other reared material available for this study. Often these small samples bridged a gap between clusters of samples. Because of the difficulty in obtaining reared, associated immature stages and adults and since the adults alone cannot be correctly placed, little reason could be mustered for the deletion of the small samples; however, the effect of small sample sizes on the significance tests is noted in appropriate places.

Tests of significance among samples were performed by the simultaneous testing procedure developed by Gabriel (1967). Simultaneous testing procedures allow one to test the homogeneity of all subsets and have the advantage that if a certain set of means is found to be not significantly different, no subset within it will be significantly different.

In addition to its application in studies of geographic variation, use of generalized discriminant functions also provides a method for finding characters to differentiate between sexes, morphs or species. In many instances, taxonomists are faced with a situation where one or two characters will not suffice to discriminate between groups with a significantly small percentage of misclassification. In the females of *Selfia,* the absence of qualitative characters, e.g., a pattern of wing spots or the shape of the spermathecae, together with a considerable amount of intraspecific variation in various quantitative characters, necessitated the search for combinations of characters which, when given appropriate weighting, would effectively discriminate between the taxa.

A large suite of characters was selected from the females in an attempt to find combinations of variables that would discriminate among four species, *hieroglyphicus, denningi, jamesi* and *jacksoni.* These characters were chosen from as many parts of the body as possible so as to measure a variety of taxonomic contrasts. About 350 specimens were originally used, all of which had been reared from larvae or pupae so that their identity as judged by the immature stages was assured, and individuals shown to be hybrids by principal components analysis were excluded.

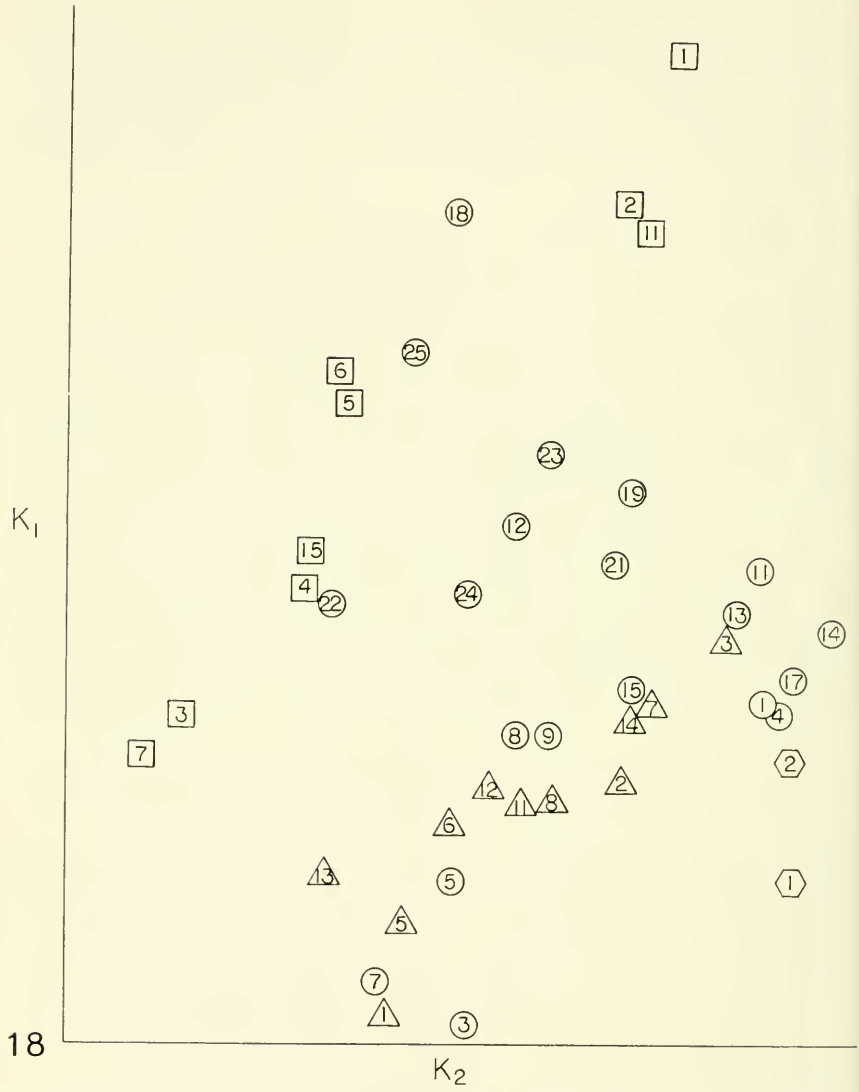

FIG. 18. Projection of group means of 42 samples of females of four species of *Selfia* onto discriminant functions. K_1 and K_2 explain 66.2% of the variance. Squares=*C. denningi,* triangles=*C. hieroglyphicus,* circles=*C. jamesi* and hexagons=*C. jacksoni.* Numbers within the symbols refer to specific localities given in Tables 4, 10 and 18.

Of the specimens of *jamesi,* 70.9% were correctly identified on the basis of the 25 adult characters, 14.2% were misidentified as *denningi,* 10.1% as *hieroglyphicus* and 4.7% as *jacksoni.* Of the remaining three species, only a small percentage was considered to be misdetermined, each time as *jamesi.*

This amounted to 10% (two specimens) of *jacksoni*, 3% of *hieroglyphicus* and 5.2% of the *denningi* material.

Numerous combinations of variables were employed with their coefficients of discrimination in an attempt to find characters to separate the females of the various taxa. This proved to be futile. If one has only adult specimens and cannot resort to the immature stages, then the females of five of the species (including *tenuistylus*) must be considered inseparable. A linear equation containing nine variables was finally found to give a fair separation, but still resulted in misdetermination of approximately 25-30% of the specimens. In view of the time involved in the solution of a nine-element equation each time one wished to identify a particular specimen, the end did not justify the means. To demonstrate the overlap in characters of females of four species, the first two discriminant functions of a number of populations were plotted (Fig. 18). This scattergram, which is based on 25 characters, amply demonstrates the difficulty in distinguishing the various species.

The second multivariate technique used to analyze variation was principal components analysis. This type of factor analysis, which examines within-group variation, is a useful summarization technique when one has a large number of correlated variables containing redundancy. These variables are reduced to a new set of dimensions, the principal components, thus ridding the data of redundancy. The factors that are extracted are orthogonal and are generally held to represent independent patterns of variation.

If one envisions a general factor model, the total variance (S^2) is composed of: 1) the *communality* (h^2) of a variable, which is given by the sum of the squares of the common factor coefficients; and 2) the *uniqueness* (d^2), which is the contribution of the unique factors. The latter can be divided into two portions of variance: 1) the *specificity* (b^2) of the variable, which is information specific to the test; and 2) the *error* variance (e^2), which is due to imperfections of measurement. Therefore, the additive property of variance can be expressed as follows:

$$S_j^2 = I = h_j^2 + d_j^2 = h_j^2 + b_j^2 + e_j^2$$

An important distinction between principal components analysis and what is generally regarded as factor analysis is that the former rescales *all* the information (including error) which distinguishes it from the analysis of common information (h^2).

The first task of a principal components analysis is to find an axis through the maximum dispersion in a hyperellipsoid formed by a multidimensional scattergram representing the states of the n characters for x species. Next, a second axis is found orthogonal to the first and in the direction of the second greatest dispersion. Then a third axis, orthogonal to the first two, is found, and so on until as much of the variance as possible is explained.

The first principal component (Y_1) of a complex of sample values for characters $X_i \ldots X_p$, therefore is a normalized linear compound $Y_1 = a_{i1}X_i + \ldots + a_{p1}X_p$ whose coefficients (a_{i1}) are the elements of the characteristic vector associated with the greatest characteristic root. The coefficients for the n characters in root 1 denote the relative importance of each original variate in the newly derived compound. The eigenvector is normalized and thus the sum of squares of the coefficients equals one. The percent of variation explained by the first root, for example, is obtained by dividing the first eigenvalue by the sum of all eigenvalues.

Factors were extracted from a character correlation matrix by the Wilkenson-Householder method, which finds the eigenvalues and eigenvectors of a matrix. The data had been previously standardized so that the characters had a mean of zero and a variance of unity. Provisions were made for missing data. The extraction of factors using method results in maximal loadings and minimal residues at every step. A more rigorous account of principal components analysis can be found in the works of Harmon (1960) and Seal (1964).

Computations of both the principal components and generalized discriminant functions were carried out on a GE 625 computer using a series of programs called NTSYS, a system for multivariate analysis, written by Dr. F. James Rohlf, John Kishpaugh and R. L. Bartcher. These programs are available at The Computation Center of The University of Kansas.

Principal components have been used to study size and shape variation by Blackith (1960), Blair *et al.* (1964) and Jolicoeur and Mosimann (1960), although there is considerable disagreement as to the usefulness of principal components in such endeavors. Blackith (1960) has pointed out that "any correlation matrix can be factorized to reveal the patterns of growth and development, the interlocking of which accounts for the observed correlations." In general, however, biologically identifiable factors that account for statistically significant fractions of the total variability of the organism are usually rather few in number and often can be rather obscure. To gain a clearer understanding of the underlying biological structure, some workers feel the factor matrix should be rotated to simple structure.

In this study, principal components were used to analyze intraspecific variation in adults and pupae of three species, *hieroglyphicus, denningi* and *jamesi,* and to test for natural hybridization among these taxa. To achieve these ends, 45 pupal and adult characters from females and 36 from males were selected to represent populational differences and intraspecific trends in variation. These are not necessarily those structures which might be used to construct a classification. The majority of the characters selected were continuous variables, due to the lack of discontinuous characters, but also because Ramon (1968) and Jackson (pers. com.) have shown that the use

of a large number of morphologically constant structures, e.g., those of the male genitalia, can obscure patterns of geographic variation and give conflicting results in cases of hybridization. Ratios were not included since they are seldom normally distributed.

From the list of these variables (Table 23) a smaller subset of adult structures was chosen for examination by generalized discriminant functions, as discussed earlier. The characters employed in this analysis are marked with an asterisk and are listed here. The number in the vector diagrams corresponds to the number of the character given here. The characters on the males were: 1) wing length; 2) wing width; 3) costa length; 4) total number of sensory pits on both antennae; 5) length of third palpal segment; 6) hind femur length; 7) hind tibia length; 8) hind basitarsus length; 9) telomere length; and 10) width of telomere apex. In females the following characters were chosen: 1) wing length; 2) wing width; 3) costa length; 4) flagellum length; 5) length of distal five flagellomeres; 6) length of proximal eight flagellomeres; 7) total number of sensory pits on both antennae; 8) head and proboscis length; 9) head length; 10) proboscis length; 11) total number of maxillary teeth from both maxilla; 12) length of third palpal segment; 13) width of third palpal segment; 14) hind femur length; 15) hind tibia length; and 16) hind basitarsus length.

The projection of population means onto the first three principal components often complemented the relationship among samples, shown by the generalized discriminant functions of adults. However, since the pupal stage is included, the principal components analysis sometimes gave results inconsistent with those of the discriminant function method, e.g., in the Kern County, California, sample of *hieroglyphicus*. For a detailed account of the discrepancy between adults and pupae in *Selfia* see Atchley (1970).

In the species descriptions, the distribution of *multipunctatus* is given only by county, while the distribution records of the remaining species are given in more detail. Since *multipunctatus* is primarily an eastern and mideastern form, the use of counties is sufficient because, in general, eastern counties are small and do not encompass marked ecological differences. The western counties, however, are generally larger and may include striking ecological changes, e.g., Riverside County, California, includes gradients from deserts to forests above 12,000 feet in elevation.

Lengths of body parts in the descriptions are listed as follows: mean (range, standard deviation; sample size). Standard deviations are not given for ratios. With regard to the proportions of the antennal flagellomeres and maxillary palps, the values given are means and, in general, the sample size is the same as that for the length of the flagellum and shape of the third

palpal segment. Range of variation and sample size is not listed for the lengths of the spermathecae since these structures are often quite difficult to measure and variation in some cases may represent mounting technique rather than intrinsic variation.

Key to Adult Females

1. Femorotibial joint pale; hind tibial comb with spine nearest spur much stouter and longer than other three; third palpal segment generally with shallow pit; multiple sensory pits on antennomeres 3, 7-10 ..... *multipunctatus*
   Femorotibial joint dark; hind tibial comb without distinctly enlarged spine; third palpal segment with deep pit; flagellum lacking regular pattern of multiple sensory pits 2
2(1). Basal four hind tarsomeres lacking distal spine; proboscis short, HR=1.3, third palpal segment very short, broad (Fig. 58) ..... *brookmani*
   Basal four hind tarsomeres with distal spine; proboscis and third palpal segment longer 3
3(2). Flagellum with sensory pits on antennomeres 3, 7-10; eyes rather widely separated, width of separation equal to 0.4-0.8 of length .... *denningi*
   Sensory pits on antennomeres 3-10 or 3, 5-10; eyes not as widely separated ..... *hieroglyphicus** *jamesi** *tenuistylus** *jacksoni**

Key to Adult Males

1. Aedeagus distally tripartite, with a collar-like structure arising from approximately midway on the aedeagal arms; claspettes with posterior process lobe-like, divided ..... *multipunctatus*
   Aedeagus with apex single, lacking collar; claspettes with posterior process not divided 2
2(1). Aedeagal arms comprised of a pair of boomerang-shaped sclerites, median posterior part of aedeagus joined to arms just posterior to caudal bend in sclerite; claspettes with median posterior process hemispherical, less heavily sclerotized than anterior arms; aedeagal membrane spiculate ..... *brookmani*
   Aedeagal arms simple, not boomerang-shaped; claspettes not as above; aedeagal membrane bare 3
3(2). Posterior margin of ninth sternum bearing a pair of caudally projecting lobes; inner face of basimere with dense patch of setae; basimeric root simple, lacking hook-like process on posterior surface 4
   Posterior margin of ninth sternum lacking lobes; inner face of

* The females of these four species can be distinguished only on the basis of the immature stages.

basimere with only normal amount of setae; basimeric root with posterior hook-like process 5

4(3). Lobes of ninth sternum elongate, extending to about middle of median portion of aedeagus, sternum divided; posterior process of claspettes elongate, about as long as body of claspettes; apex of telomere with lateral projection often becoming foot-shaped ..... *hieroglyphicus*

Lobes of ninth sternum not as well developed, barely extending as far as anterior end of basimere; median process of claspettes short, rounded; apex of telomere at best only slightly expanded .... *denningi*

5(3). Ninth sternum with posterior margin straight, lacking cleft or emargination; claspettes lacking median posterior elongation; a globular projection in recess of hook-like process on basimeric root ..... *tenuistylus*

Ninth sternum with posterior margin either cleft or emarginate; posterior portion of claspettes very much elongated; globular process lacking 6

6(5). Apex of telomere markedly foot-shaped; rugose membrane arising from posterior margin of basimeric root and attaching to aedeagus; aedeagus not eversible, with subapical constriction, lacking horizontal piece connecting arms ..... *jamesi*

Apex of telomere at best only slightly expanded; posterior margin of root lacking membrane; aedeagus eversible, tapering posteriorly with a horizontal cross-piece connecting arms at about mid-length ..... *jacksoni*

Key to Pupae

1. Respiratory horn ham-shaped (Fig. 65), with numerous spiracular openings in J-shaped pattern following trachea; some *lpm* and *lasm* spines often bi- or trifed, swollen or bent; operculum with only a few teeth ..... *brookmani*

Respiratory horn slender, not as above; *lpm* and *lasm* spines with simple apices 2

2(1). Respiratory horn with four lateral spiracular openings arising from armed protuberance (Fig. 40); one pair of *vm* spines present; males lacking mesal lobe at base of genital sheaths on ninth segment ..... *multipunctatus*

Respiratory horn with two or three lateral spiracular openings, lacking armed protuberances; two pair of *vm* spines present; mesal lobe at base of genital sheaths present in males 3

3(2). Abdomen with bases of *lpm* tubercles spiniform; spine d_3 short, about 5μ in length 4

Abdomen with bases of *lpm* tubercles rounded; spine d_3 longer, about 13μ in length 5

4(3). Abdomen with up to six segments bearing spiniform *lpm* tubercles; respiratory horn short, averaging about 170μ; operculum generally lacking outer row of stronger teeth; *am* spine/operculum width=4.7-5.1 ..... *denningi*
Abdomen with spiniform *lpm* tubercles usually on only one or two segments; respiratory horn longer, averaging about 200μ in length; operculum with outer row of larger, stronger teeth; *am* spine/operculum width=4.0 ..... *hieroglyphicus*

5(3). Respiratory horn with three lateral spiracular openings; operculum with very dense teeth, extending well beyond base of *am* spine (Fig. 229) ..... *jamesi*
Respiratory horn with two lateral spiracular openings; operculum with teeth less dense and extending to about level of base of *am* spine 5

6(5). Respiratory horn long, averaging 215μ; *am* d_1 and *ad* spines long (see Table 5); found in Utah, New Mexico and Arizona ..... *jacksoni*
Respiratory horn shorter, averaging 190μ; *am*, d_1 and *ad* spines shorter; restricted to California ..... *tenuistylus*

Culicoides (Selfia) multipunctatus Complex

The *multipunctatus* complex comprises *multipunctatus* and *brookmani*. At first glance these two species might appear to have little in common because *multipunctatus* has retained a number of pleisiomorphous features, while *brookmani* exhibits several strikingly apomorphous structures. As explained earlier, this is apparently due to the early divergence of the two forms. In spite of this seeming dissimilarity, I have placed these two species in the same group on the basis of the following characteristics.

Both *multipunctatus* and *brookmani* have the basal portion of the basimere markedly expanded and containing a slender, apically curved basimeric root. In *multipunctatus* the root has a small process on the posterior surface. The apicolateral processes of the ninth tergum in both species are small and more or less triangular and the ninth sternum is posteriorly emarginate. The claspettes have a lobe-like posterior process, which is divided in *multipunctatus*.

The scutellum in the females of both species is devoid of microsetae and there is no mesal thumb-like lobe on the ninth sternum.

The apices of the *lpm* and *lasm* tubercles on the pupal abdomen are spiniform on nearly all segments. Further, most of the tubercles of the head and thorax are spiniform. The last segment of the male pupa lacks the mesal lobe found between the genital sheaths in other species of *Selfia*.

The larvae are unknown.

The geographic distribution of *multipunctatus* and *brookmani* is given in Figure 19.

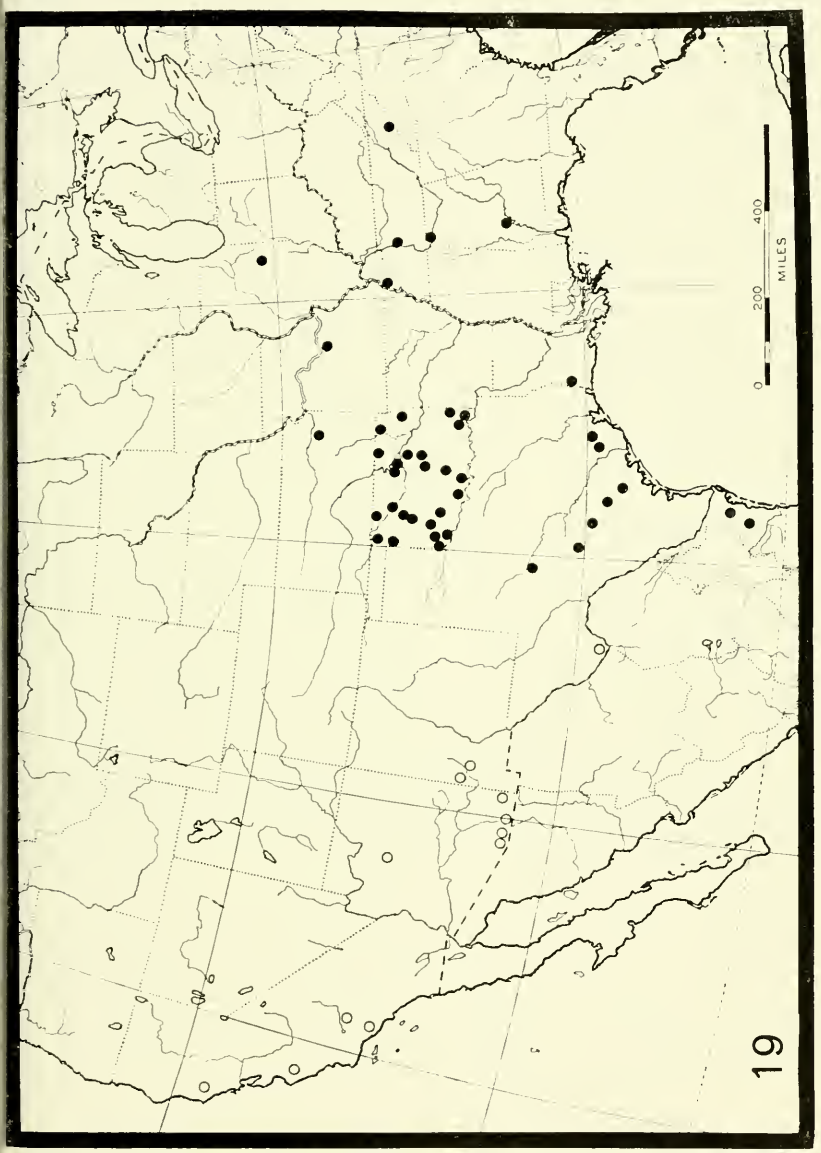

Fig. 19. Known distribution of the *C. multipunctatus* complex. Closed circles=*C. multipunctatus*, open circles=*C. brookmani*.

Culicoides (Selfia) multipunctatus Malloch
(Figs. 1, 20-53)

Culicoides multipunctatus Malloch, 1915, Ill. State Lab. Nat. Hist. Bull. 10:296 (female; Illinois).
Culicoides (Selfia) multipunctatus, Khalaf, 1954, 38.

The description of the adults of this species is based on a collection of over 100 specimens from Kerrville, Texas, while the pupae are described from 25 specimens reared from Payne County, Oklahoma, and Meade County, Kansas.

FEMALE—Length of wing 0.85 mm (0.76-0.91, ±0.046; n=14); width 0.43 mm (0.38-0.48, ±0.027; n=14).

Head: Vertex with numerous long setae. Eyes only moderately widely separated (Fig. 1), width of separation equal to 0.34 (0.23-0.50) of length. Antennal flagellomeres in proportion of 10:7:7:7:7:7:8:8:9:10:10:12:20; proximal eight flagellomeres roughly 1.2 times as long as broad (Fig. 38); total length of flagellum 406μ (372-425, ±17.3; n=14); antennal ratio 0.96 (0.90-1.01; n=14); antennomeres 9+10 to 11 in ratio of 0.62 (0.56-0.69; n=14); distal sensory pits present on antennomeres 3, 5-10, occasionally present on 4; multiple sensory pits on antennomeres 3, 7-10, occasionally on 5 and/or 6. Distal four palpal segments in proportion 13:19:8:9; third segment moderately swollen, 2.1 (2.0-2.3; n=14) times as long as greatest breadth, generally with shallow sensory organ (Fig. 28), sometimes with deep organ (Figs. 30-32 for variation). Total length of head 301μ (282-319, ±10.0; n=15); ratio of head length to proboscis 1.16 (1.06-1.29; n=15); tormae broad, bladelike. Mandibles with 12 (10-13) teeth. Maxillae with 14 (12-16) teeth.

Thorax: Mesothorax pruinose gray with pattern of dark brown punctiform dots most evident in mesal third of notal disc; dots sometimes coalescing to rather distinct vittae. Legs brownish, femorotibial joint pale; coxa, trochanter and apex of femur pale, remainder of leg darker; basal portion of femur and tarsomeres sometimes slightly paler, often most prevalent on hind leg. Hind leg segments and tarsomeres in proportion of 46:20:109:101:54:25:16:11:14; hind tibial comb with four spines, spine nearest spur much stouter and longer than other three; first four hind tarsomeres with distal spine. Scutellum with one pair median and one pair lateral macrosetae; microsetae absent (Fig. 36). Stigma of wing brownish. Macrotrichia occurring over majority of wing but sparser in posterior portions. Costa extending 0.55 (0.51-0.57; n=14) of entire wing length.

Abdomen: Brown. Eighth sternum with shallow median posterior pocket; lateral edges of pocket simple, unmodified (Fig. 24). Ninth sternum lacking thumb-like lobe. Spermathecae three, subequal, more heavily sclerotized than in other *Selfia* species (Fig. 25); bursa with three separate distal openings (Figs. 26-27); spermathecae with basal one-fourth swollen

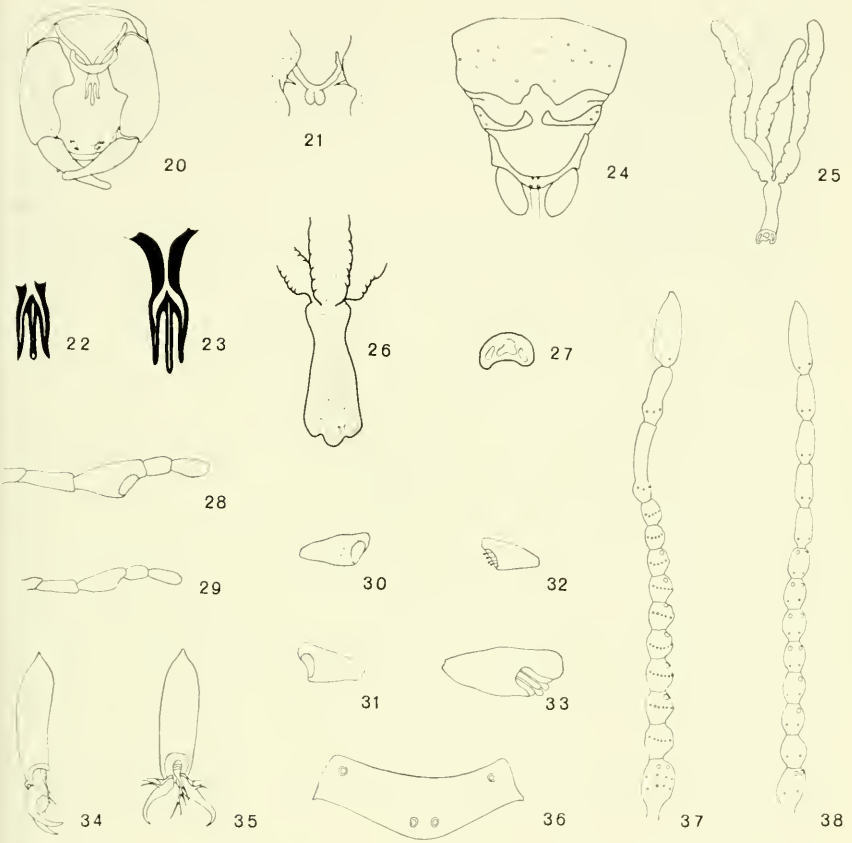

Fig. **20-38.** *Culicoides (Selfia) multipunctatus* Malloch. **20,** male genitalia, claspettes removed; **21,** apex of aedeagus; **24,** ventral view abdominal segments 8-10 of female; **25,** spermathecae; **26,** bursa; **27,** apex of bursa showing three separate openings; **28,** female palpus; **29,** male palpus; **30-32,** variation in third palpal segment of female; **33,** third palpal segment of male; **34-35,** pre-tarsal claw of female; **36,** scutellum of female; **37,** flagellum of male; **38,** flagellum of female.

(more evident in some specimens than others) and joined to bursa by very short duct; slight indication of constriction separating bulbous basal portion from apical three-fourths; spermathecae 136, 149 and 151μ long, respectively; bursa about 59μ long. (Considerable amount of intrapopulational variation exists with respect to the length of spermathecal system as a whole; many specimens with system appearing very short and compact.)

MALE—Length of wing 0.71 mm (0.66-0.74, $\pm$0.027; n=9); width 0.31 mm (0.30-0.33, $\pm$0.012; n=9).

Head: Appendages sometimes slightly paler than head capsule; distal three flagellomeres of antenna darker than preceding 10. Antennal flagello-

meres in proportion of 15:9:9:8:8:7:7:7:7:7:23:16:20 (Fig. 37); distal sensory pits present on antennomeres 3, 7-10, often on 5 and 6; multiple sensory pits sometimes present on other than 3; flagellum length 443μ (422-465, $\pm$14.9; n=8). Distal four palpal segments in proportion of 10:15:7:10, third segment with small, deep sensory organ (Fig. 29). Head length 288μ (273-310, $\pm$14.4; n=7).

Thorax: Mesonotal pattern and leg coloration as in females. Hind leg with segments in proportion of 45:20:98:90:48:24:15:10:13; hind tibial comb as in females. Scutellum with one pair lateral and one pair median macrosetae; microsetae absent. Macrotrichia sparse, confined to distal portions of wing. Costa extending 0.47 (0.45-0.48; n=9) of entire wing length.

Genitalia (Figs. 20-21): Ninth tergum tapered caudally, with a pair of small subapical, setigerous lobes; apicolateral processes rather short, slender, divergent; posterior margin with only slight mesal notch. Ninth sternum with very deep, wide, posteromedial emargination. Anterior half of basimere markedly expanded, distinctly narrowed at midlength producing prominent shelf; numerous long setae arising from expanded basal portion; dense patch of setae lacking on inner face of basimere; basimeric root elongate, slender, slightly recurved, with distinct, pointed, mesally projecting, faintly curved, blade-like process arising on anteromedial margin and resting on "shoulder" of claspette. Telomere slightly swollen basally, tapering distally to slender, simple, apex; base often with dense covering of long setae. Aedeagus tripartite; median process longer than two faintly divergent lateral ones; arms slender and more or less straight except for slight anterior bend at apex; collar arising from midpoint of arms and extending about one-third length of median posterior portion. Claspettes fused (Fig. 21); two prominent, oblong, median, posterior, lobiform processes present; anterior process usually faintly sinuate, sometimes arcuate, with prominent lateral shoulders and high mesal arch.

PUPA: Light brown.

Respiratory horn (Fig. 39): Arising from raised pedicel and containing a single trachea. Apex dark, approximately same width as remainder of horn. Four lateral spiracles opening on conspicuous, well-separated, slightly darker protuberances, basal one not as distinctive as other three; protuberances bearing one or two acute spines (Fig. 40). Lateral convolutions generally most distinct distal to last spiracle opening.

Operculum (Fig. 41-42): Brown; markedly denticulate; very strong teeth on lateral margins, particularly at approximate midpoint of outermost row; teeth projecting posteriorly between *am* tubercles. Tubercles well developed and possessing long spines.

Cephalic-thoracic chaetotaxy: Base of antennal pad and *ad* tubercle only slightly darker than apex of pad. Tubercles d_3, d_4, *dl*, *vl* and *vm* with bases

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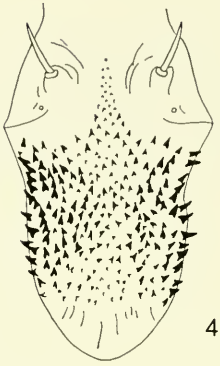

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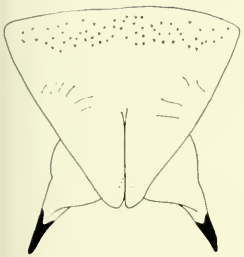

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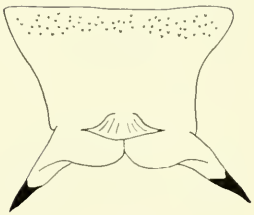

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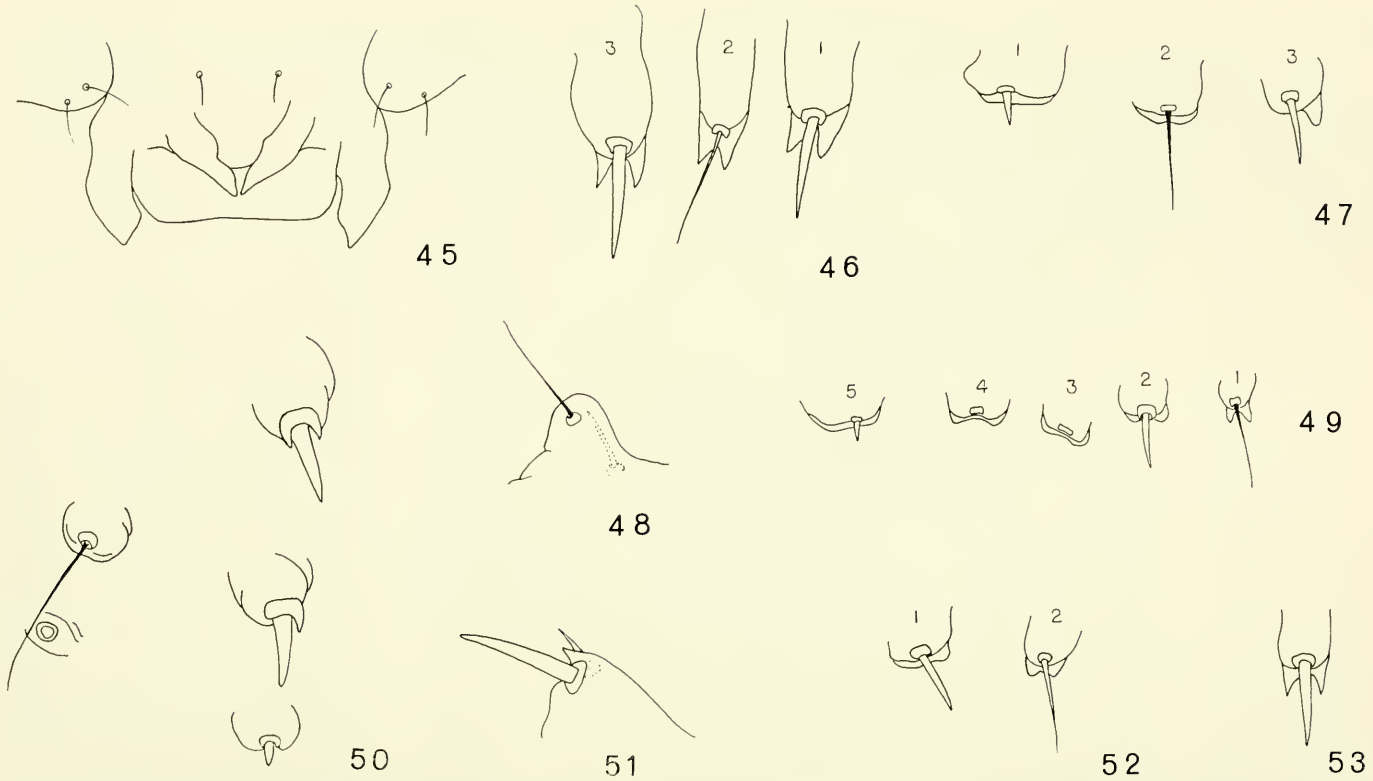
Figs. **39-44.** *Culicoides (Selfia) multipunctatus* Malloch. **39,** pupal respiratory horn; **40,** armed protuberance of horn; **41,** female operculum; **42,** silhouette of opercular teeth; **43,** last abdominal segment of male pupa; **44,** last abdominal segment of female.

rounded; remainder of tubercles with spiniform bases. *Dorsal* tubercles with spine of d_1 never overlapping d_2 (Fig. 50); distance between sockets of d_1 and d_2 greater than distance between d_2 and d_3 (see Table 1). Tubercle *ad* with one large, stout spine and second smaller, shorter spine (Fig. 51). Tubercle *dl* with two spines (Fig. 48). Two pairs of *vl* spines present; only one pair of *vm* spines (Fig. 45).

Abdomen: All *lpm* and *lasm* tubercles with conspicuously spiniform bases on segments 3-8 (Figs. 46, 53); *dpm* tubercles with spines lacking on segments 3 and 4 (Fig. 49); *vpm* tubercles as in Figure 47; *dasm* tubercles as in Figure 52. Last segment of male with long, simple genital sheaths, lacking any type of distal modification (Fig. 43); mesal lobe at base of genital sheaths absent (Figs. 43-44).



FIGS. **45-53.** *Culicoides (Selfia) multipunctatus* Malloch. **45,** *vm* and *vl* setae; **46,** *lpm* tubercles; **47,** *vpm* tubercles; **48,** *dl* tubercle; **49,** *dpm* tubercles; **50,** *d* tubercles; **51,** *ad* tubercle; **52,** *dasm* tubercles; **53,** *lasm* tubercle.

LARVA: Unknown.

DISTRIBUTION:

This species is distributed by state and county as follows: ALABAMA: Lauderdale, Wilcox counties. ILLINOIS: Champaign County. KANSAS: Douglas County. LOUISIANA: Calcasieu Parish. MISSOURI: Boone County. OKLAHOMA: Beckham, Canadian, Cleveland, Comanche, Creek, Custer, Delaware, Ellis, Grant, Greer, Harmon, Harper, Jackson, Jefferson, Kingfisher, LeFlore, Love, Major, McCurtain, McIntosh, Murray, Noble, Nowata, Okfuskee, Osage, Pawnee, Pushmataha, Seminole, Woods counties. TENNESSEE: Cocke, Humphreys, Lake, Obion counties. TEXAS: Bexar, Fort Bend, Karnes, Kerr, Sterling, Sutton counties. MEXICO: Tamaulipas.

DISCUSSION: Khalaf (1952), in a study of the *Culicoides* of the Wichita Mountains Wildlife Refuge, Oklahoma, described the male of *multipunctatus* but designated one specimen as an allotype and several others as paratypes. Since allotypes and paratypes are by definition part of the original type series, the specimens designated as types by Khalaf can have no status.

Culicoides (Selfia) brookmani Wirth

(Figs. 54-82)

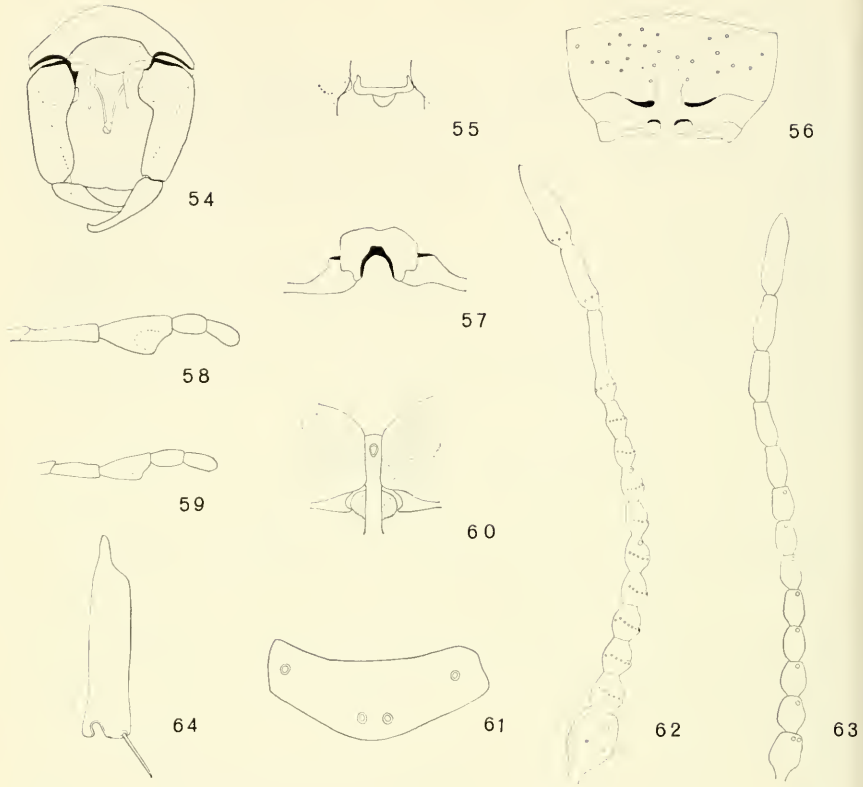
Culicoides brookmani Wirth, 1952, Univ. Calif. Publ. Ent. 9:179-180 (male, female; Arroyo Seco R. S., Monterey Co., Calif.; fig. wing, palpus, male genitalia).
Culicoides (Selfia) brookmani; Khalaf, 1954, 38.

The description of this species is based primarily on approximately 50 reared and light trap specimens from Sedona, Arizona.

FEMALE—Length of wing 0.95 (0.90-1.0, ±0.04; n=10); width 0.47 mm (0.44-0.48, ±0.01; n=10).

Head: Vertex with numerous long setae. Separation between eyes long, narrow, about 0.13-0.20 times as wide as long (Fig. 60). Antennal flagellomeres in proportion of 10:9:9:9:9:9:9:10:12:14:15:22; proximal eight flagellomeres roughly 1.8 times as long as broad (Fig. 63); total length of flagellum 446μ (409-468, ±18.1; n=10); antennal ratio 0.93 (0.88-0.97; n=10); antennomeres 9+10 to 11 in ratio of 0.57 (0.53-0.61; n=10); distal sensory pits on antennomeres 3-10, occasionally absent from 4; multiple sensory pits occasionally present on antennomeres other than 3. Distal four palpal segments in proportion of 16:18:9:10; third segment very short, swollen, 1.9 (1.8-2.1; n=10) times as long as greatest breadth, with a deep sensory organ (Fig. 58). Total length of head 314μ (301-329, ±8.2; n=10); ratio of head length to proboscis 1.30 (1.11-1.46; n=10). Tormae very slender. Mandibles with 12 (10-12) teeth. Maxillae with 14 (12-15) teeth.

Thorax: Mesonotum dark brown with rather indistinct lighter brown markings; a median dark stripe with abutting, slightly paler, brown bands, the latter each bordered by pair of narrow dark stripes, apparently originating at mesal edge of humeral pits. Legs brown; femorotibial joint dark; occasionally faint subbasal pale band on fore tibia. Hind legs with segments in proportion of 45:20:114:109:55:25:16:10:13; hind tibial comb with four,



FIGS. **54-64.** *Culicoides (Selfia) brookmani* Wirth. **54,** male genitalia, claspettes removed; **55,** claspettes; **56,** eighth and ninth sternum of female; **57,** ninth sternum and gonopore of female; **58,** female palpus; **59,** male palpus; **60,** female eye separation; **61,** female scutellum; **62,** male flagellum; **63,** female flagellum; **64,** fore tarsomere of female.

rarely five, spines, no one spine distinctly longer than any other; basal four hind tarsomeres lacking distal spine. Scutellum with one pair median, one pair lateral macrosetae; microsetae absent (Fig. 62). Stigma of wing pale brown, often somewhat indistinct. Macrotrichia short, present on most cells and veins but sparse. Costa extending 0.53 (0.51-0.56; n=10) of entire wing length.

Abdomen: Brown. Eighth sternum with posteromedian pocket extending somewhat less than half length of segment (Fig. 56); posterolateral margins of pocket forming dark, unmodified ridge, without hook-like processes. Ninth sternum with anterior and mesal faces bearing slightly heavier sclerotized band but lacking thumb-like anterior projections. Spermathecae virtually unsclerotized, very difficult to see even with phase-contrast microscopy; apparently three in number, but little as to shape, etc., can be ascertained;

external opening of bursa broad, distinctly U-shaped (Fig. 57), bursa approximately 30μ long; mesal faces of divided ninth sternum appressed against apical ends of opening.

MALE—Length of wing 0.82 mm (0.77-0.85, $\pm$0.002; n=8); width 0.36 mm (0.34-0.37, $\pm$0.001; n=7).

Head: Brown. Antennal flagellomeres in proportion of 15:10:10:9:9:8:8: 8:8:8:25:18:25 (Fig. 62); distal sensory pits present on antennomeres 3, 6, 8 and 10, occasionally absent from 6; multiple pits lacking; flagellar length 502μ (474-536, $\pm$18.9; n=8). Distal four palpal segments in proportion of 12:14:9:10 (Fig. 59); third segment with small, deep sensory organ. Head length 303μ (294-316, $\pm$9.2; n=7).

Thorax: Legs light brown, paler than in female; femorotibial joint dark; faint subbasal pale band often on fore tibia. Hind leg with segments in proportion of 45:20:106:100:51:25:16:10:13; hind tibial comb with four spines, one leg rarely with three; basal four hind tarsomeres lacking distal spine. Scutellum as in female. Stigma of wing very faint brownish. Macrotrichia short, quite sparse and confined to anterior portion of cell R_5, distal portion of M_1 and occasionally M_2; absent from M_4 and vannal cell. Costa extending 0.45 (0.43-0.46; n=8) of entire wing length.

Genitalia (Figs. 54-55): Ninth tergum narrowed caudally, with slight median posterior notch; apicolateral processes short, triangular. Ninth sternum with rather broad posterior emargination; posterolateral corners modified into sclerotized cups where anterior end of basimere articulates; anterior margin of segment rounded. Basimere oblong with moderate setation; anterior end distinctly expanded, shelf produced at point of submedian constriction, posteromedian corner with prominent notch apparently where lateral portion of aedeagus rests; basimeric root slender, slightly curved distally, arising at anterior margin of expanded basal portion of basimere; no evidence of second root-like process on anterior surface as in *multipunctatus*. Telomere with slender, spined apex. Lateral arms of aedeagus formed from pair of peculiar, boomerang-shaped sclerites, the latter expanded at their outer ends, median posterior process triangular, attached to boomerang-shaped sclerites at point just anterior to posterior bend in sclerites; median process bounded laterally by thin, but heavily sclerotized stripes, apex thin and recurved; aedeagal membrane densely spiculate. Claspettes fused (Fig. 55); median posterior part hemispherical in shape, much less heavily sclerotized than arms; anterior processes horizontal with anteriorly directed, pointed ends. Lateral boomerang-shaped aedeagal sclerites, recurved apex and fused claspettes form a distinct "pocket."

PUPA: Yellowish brown to light brown. Quantitative characters are summarized in Table 2.

Respiratory horn (Fig. 65): A peculiar ham-shaped structure originating

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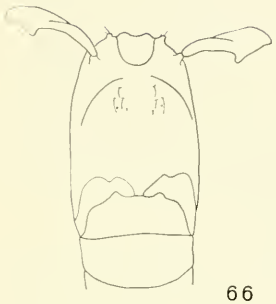

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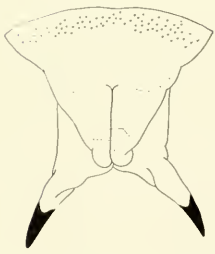

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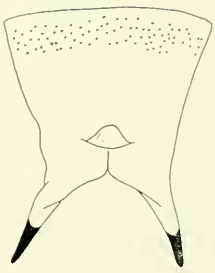

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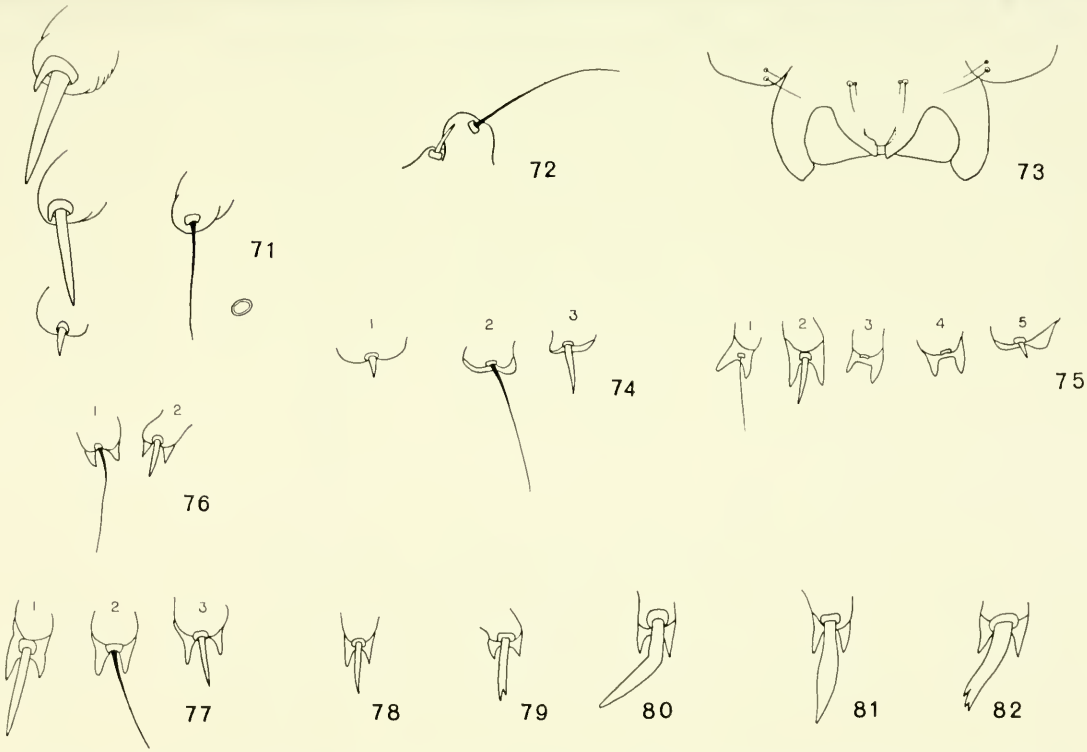
FIGS. **65-70.** *Culicoides (Selfia) brookmani* Wirth. **65,** pupal respiratory horn; **66,** thorax and respiratory horns; **67,** silhouette of opercular teeth; **68,** female operculum; **69,** last abdominal segment of male pupa; **70,** last abdominal segment of female.

from raised pedicel; proximal third narrower than greatly expanded apical two-thirds, apex approximately 170μ wide and slightly cupped (Fig. 66); horn thin, blade-like when viewed from side and apparently composed of vast number of tubes three layers thick, some tubes lying between outer layers and forming a conflicting pattern. Single trachea entering horn becomes J-shaped distally; spiracular apertures along lateral margins of basal



Figs. **71-82.** *Culicoides (Selfia) brookmani* Wirth. **71,** *d* tubercles; **72,** *dl* tubercle; **73,** *vm* and *vl* setae; **74,** *vpm* tubercles; **75,** *dpm* tubercles; **76,** *dasm* tuberces; **77,** *lpm* tubercles; **78,** *lasm* tubercle; **79,** modified *lasm* tubercle; **80-82,** modifications of *lpm* tubercles.

third, where they form apices of tubes, and along median region of J-shaped trachea; of the latter, apertures along two vertical sections of internal trachea exit on dorsal surface, with those of distal horizontal section open on ventral side.

Operculum (Figs. 67-68): Brown; denticulation reduced to a few teeth in concave pattern at approximate midlength of operculum, never extending between *am* tubercles; larger teeth confined to lateral portion of operculum; *am* tubercle well-developed, with very long, stout spine.

Cephalic-thoracic chaetotaxy: Base of antennal pad and *ad* tubercle dark. Tubercles *ad*, d_1 and d_2 with bases spiniform, other tubercles with bases rounded. Spine of d_1 overlapping tubercle of d_2, and d_2 overlapping tubercle of d_3 (Fig. 71); distance between sockets of d_1 and d_2 greater than that between d_2 and d_3; tubercle of d_4 originating at same level as d_2. Two pairs of *vl* and two pairs of *vm* spines (Fig. 73). Tubercle *dl* as in Figure 72.

Abdomen: All *lpm* and *lasm* tubercles with strongly spiniform bases (Fig. 77-78); *lpm*'s with spines often strikingly modified by having mesal portion swollen to width greater than base (Fig. 81), or being mesally bent (Fig. 80), or having apex toothed (Fig. 82); all these variations often found on the same individual; *lasm* sometimes with spine distally toothed (Fig. 79); *dpm* tubercles with bases spiniform (Fig. 75), lacking spines on tubercles 3 and 4; *dasm* tubercles often with spiniform bases (Fig. 76); *vpm* tubercles as in Figure 74. Last segment in both sexes with long, slender, divergent, posterolateral process (Figs. 69-70); genital sheaths of male with simple apices; mesal lobe at base of sheaths absent.

LARVA: Unknown.

DISTRIBUTION: This species has been recorded only from the southwestern United States, from northern California down the coast into southern California, where it is apparently more common, across the lower, drier portions of Arizona and New Mexico to the Big Bend region of Texas. It no doubt occurs commonly in northern Mexico, but there are no records from that region.

Specimens examined:

Holotype male, allotype female and 5 female paratypes, Arroyo Seco Ranger Station, Monterey County, California, 1 July 1948, W. W. Wirth, light; 1 male paratype, Piru Canyon, Ventura County, California, 22 April 1948, W. W. Wirth, light. (All type material in USNM.) Additional material examined: ARIZONA: Coconino County, Oak Creek, at Sedona, 17 June 1968, reared, 20 females, 18 males with pupal exuvia; Oak Creek Canyon, 29 June 1953, W. W. Wirth, light, 20 females, 15 males; Cochise County, Ramsey Canyon, Huachuca Mts., July 1967, light, 1 male; S. W. Res. Stat., 5 m. w. Portal, 9 Sept. 1959, light, 2 females; same locality, 23 May 1963, light, 3 females; Portal, 6 July 1956, light, 2 females; Portal, June y965, 2 males; Montezuma Well Nat'l. Mont., 2 Sept. 1953, light, 2 females; Santa Cruz County, Sycamore Canyon, Ruby, 22 May 1954, light, 16 females, 12 males; Sycamore Canyon, 10 Aug. 1968, reared, 1 female with pupal exuvium. CALIFORNIA: Kern County, Kern Canyon, 15 mi. E. Bakersfield, 6 Aug. 1964, 2 males; Lake County, Nice, 7 Oct. 1938, 1 male; Mendocino County, Hopland, 14 May 1964, *ex* ear of jackrabbit and ear of deer, 3 females; Hopland, 25 June 1964, *ex* ear of jackrabbit, 1 female; Riverside County, Deep Canyon, 17 Dec. 1963, light, 3 females. NEW MEXICO: Catron County, Glenwood Fish Hatchery, 2

August 1965, light, 1 male; 5 mi. E. Glenwood, 24 June 1953, light, 1 female, 1 male; Gila Nat'l. Mont., 14 June 1964, light, 3 females. TEXAS: Brewster County, Big Bend Nat'l. Park, Glen Springs, 7 April 1956, light, 6 females, 4 males.

Culicoides (Selfia) hieroglyphicus Complex

The *hieroglyphicus* complex includes *hieroglyphicus* and *denningi*. These two species are quite similar, particularly in the male genitalia and the immature stages.

The posterior margin of the ninth sternum of the adult male has a pair of caudally projecting lobes which are apparently unique in the genus. In *hieroglyphicus*, the lobes are more pronounced, the cleft separating them continuing anteriorly to divide the segment. The basimere in this group has a dense patch of setae on the mesal face, a sclerotized shelf at the anterior end which articulates with the aedeagal arms, and a single, apically truncate basimeric root without any hook-like modification of the posterior surface. Both species have a pair of slender, divergent aedeagal arms, and an eversible aedeagus.

There are two very long, lightly sclerotized spermathecae and a third short one. The scutellum of the females possesses microsetae.

The pupae have the *lpm* and *lasm* tubercles of the abdomen with spiniform bases; however, in *hieroglyphicus* these are usually restricted to abdominal segments 7 and 8. There is a mesal lobe between the genital sheaths on the ninth segment. Usually there are two lateral spiracular openings on the respiratory horn, but pupae of some of the more northern populations of *hieroglyphicus* often have three.

In the larvae the frontal comb of the epipharynx is distinctive in that the teeth are rounded, rather than sharp.

Culicoides denningi is a cool-adapted species found in the northwestern states and Canada and at high elevations in Utah, Nevada and Colorado. *Culicoides hieroglyphicus* is common in the southwestern states and Mexico and at lower elevations in Utah, Nevada, etc. The two species are sympatric in northeastern Utah, southeastern Wyoming and northern Colorado (Fig. 83).

Culicoides (Selfia) denningi Foote and Pratt

(Figs. 2, 8, 10, 13-17, 83-107)

Culicoides denningi Foote and Pratt, 1954, Pub. Health Monograph 18:20-21 (male, female; Saskatoon, Saskatchewan; fig. wing, mesonotal disc, palpus, male genitalia).
Culicoides (Selfia) denningi; Fox, 1955, 22.

The following description is based on an extensive paratypic and topotypic series from Saskatoon, Saskatchewan.

FEMALE—Length of wing 1.17mm (1.05-1.24, ±0.06; n=13); width 0.53 mm (0.49-0.59, ±0.04; n=12).

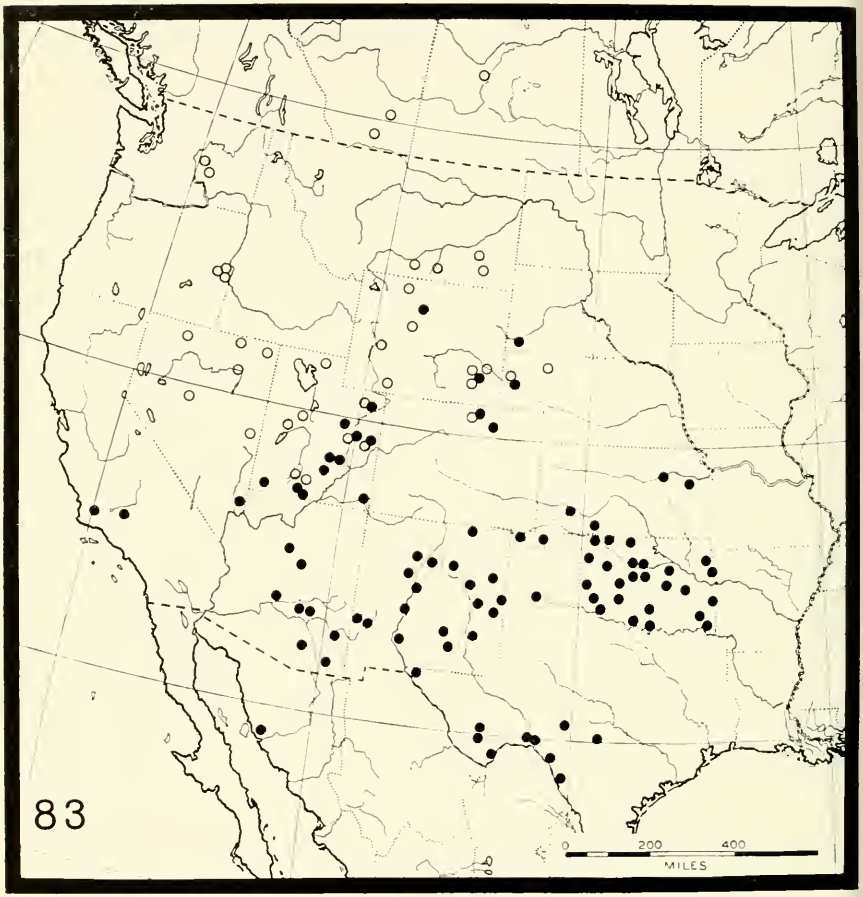
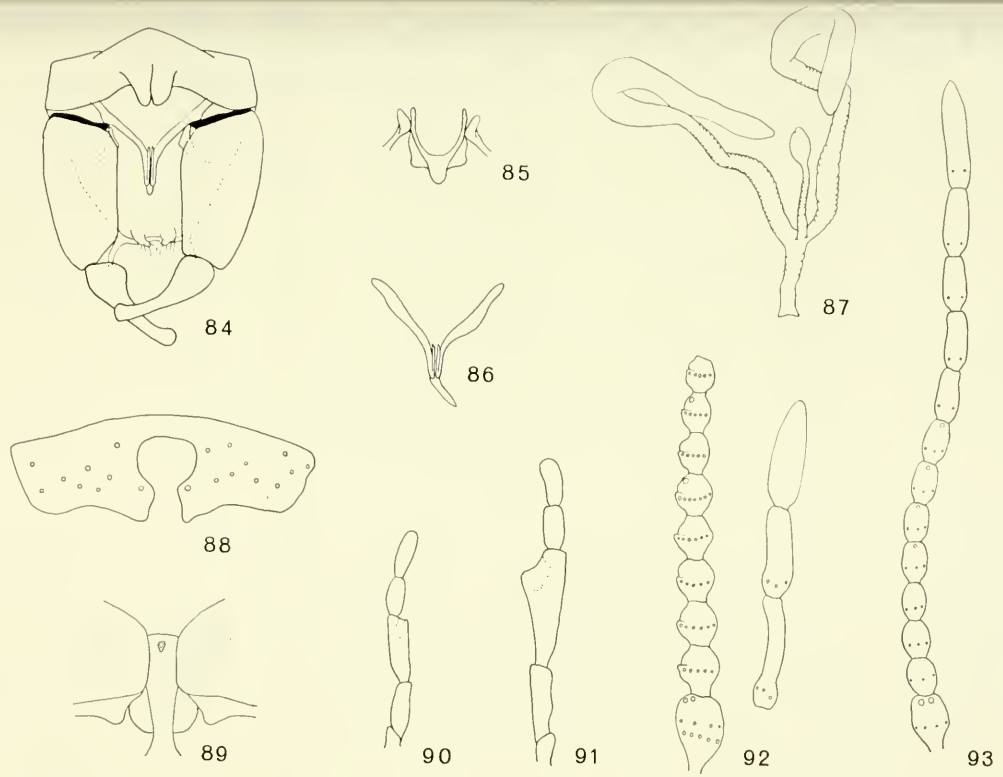


FIG. 83. Known distribution of *C. (S.) hieroglyphicus* complex. Closed circles=*C. (S.) hieroglyphicus;* open circles=*C. (S.) denningi.*

Head: Head capsule brown, antennae and palpi pale yellowish brown. Vertex with numerous long setae. Eyes generally rather widely separated, width of separation equal to 0.40-0.75 of length (Fig. 89). Antennal flagellomeres in proportion of 15:9:9:9:9:10:10:10:10:12:15:15:17:27; proximal eight flagellomeres roughly 1.5 times as long as broad (Fig. 93); total length of flagellum 482μ (465-518, $\pm$22.0; n=13); antennal ratio 1.02 (0.95-1.07; n=13); antennomeres 9+10 to 11 in ratio of 0.63 (0.56-0.70; n=13); distal sensory pits present on antennomeres 3, 7-10; multiple sensory pits present only on 3. Distal four palpal segments in proportion of 17:27:10:12; third segment moderately swollen, 2.7 (2.45-3.0; n=13) times as long as greatest breadth, with a deep sensory organ (Fig. 91). Total length of head 371μ



Figs. **84-93.** *Culicoides (Selfia) denningi* Foote and Pratt. **84,** male genitalia, claspettes removed; **85,** claspettes; **86,** aedeagus in everted position; **87,** spermathecae; **88,** eighth sternum of female; **89,** female eye separation; **90,** male palpus; **91,** female palpus; **92,** male flagellum; **93,** female flagellum.

(335-394, ±13.0; n=13); ratio of head length to proboscis 1.13 (1.04-1.18; n=13). Mandibles with 12 (11-13; n=13) teeth. Maxillae with 16 (14-18; n=13) teeth.

Thorax: Mesonotum brown with alternating brown and grayish bands: median, brown stripe bounded laterally by rather narrow, longitudinal grayish bands; submedian grayish bands in turn bordered in mesal third by short, thin, brown stripes, posteriorly expanded to lateral margins of disc; a brown stripe projected laterad from humeral pit and along lateral margin of disc, coalescing with posterolateral enlargement of outermost brown band; grayish areas at antero- and posterolateral edges of humeral pit. Legs light brown, femorotibial joint slightly darker. Fore legs with indistinct subapical femoral and subbasal tibial pale bands. Hind leg with segments in proportion of 49:20:134:132:71:33:20:12:15; hind tibial comb with four spines, occasionally one leg with five; basal four hind tarsomeres with distal spine. Scutellum with four macrosetae, two median and two lateral, and four microsetae, one pair between each median and lateral macroseta. Stigma light brown. Macrotrichia numerous over majority of cells and veins, most abundant at anterior margin of cell R_5. Costa extending 0.57 (0.55-0.60; n=13) of entire wing length.

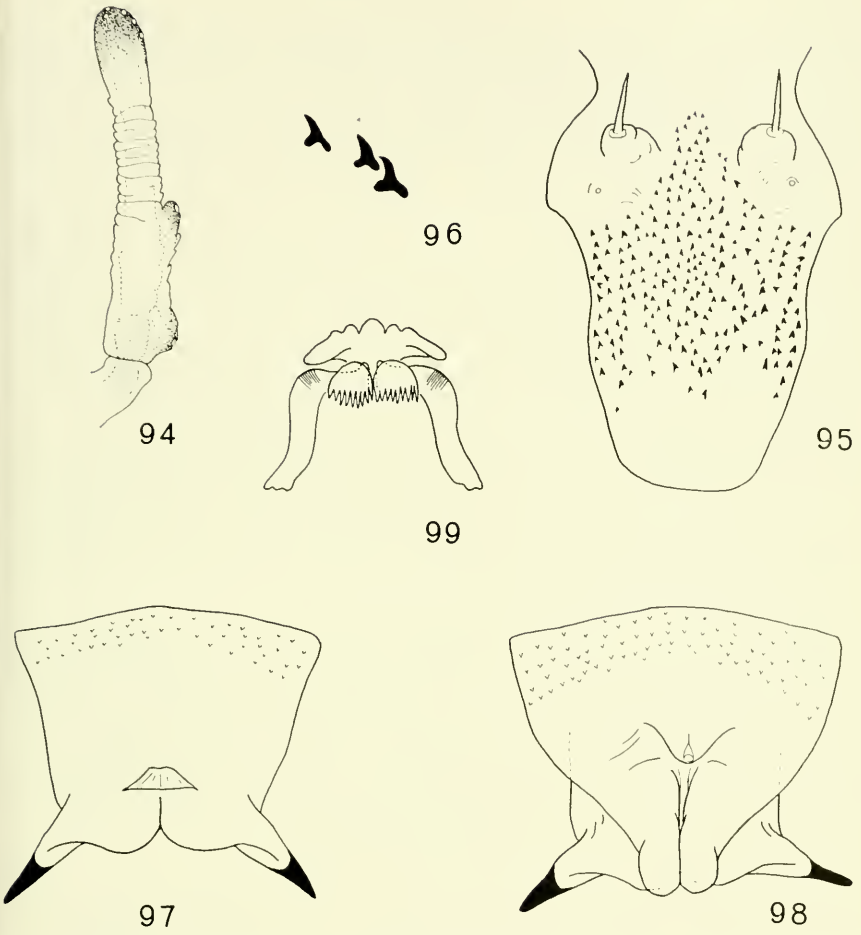
Abdomen: Yellowish brown. Eighth sternum with deep posteromedial pocket, narrowed at mouth; lateral margins of opening simple, unmodified (Fig. 88). Spermathecae three (Fig. 87): two long, digitform, usually coiled back on themselves, measuring 335 and 304μ respectively from tip to union with common duct; third smaller, thinner, distally bulbous, 62μ in length.

MALE—Length of wing 1.0 mm (0.98-1.03, ±0.03; n=11); width 0.40 mm (0.37-0.42, ±0.02; n=10).

Head: Brown, sometimes slightly darker than in female, appendages lighter than head capsule. Antennal flagellomeres in proportion of 18:10:10:9:9:9:9:9:10:27:20:25 (Fig. 92); distal sensory pits on antennomeres 3, 8 and 10; flagellar length 547μ (539-561, ±8.7; n=9). Distal four palpal segments in proportion of 11:17:10:11; third segment slightly swollen with small, deep sensory organ (Fig. 90). Head length 315μ (294-341, ±17.0; n=8).

Thorax: Leg coloration as in female. Hind leg with segments in proportion of 52:20:121:119:63:31:19:12:15; hind tibial comb with four spines. Scutellum with two median and two lateral microsetae, a single microsetae lying between median and lateral macrosetae. Stigma of wing light grayish. Macrotrichia most abundant in anterior part of wing, scarce on posterior veins and cells, usually absent in vannal cell. Costa extending 0.49 (0.47-0.52; n=11) of entire wing length.

Genitalia (Figs. 84-86): Ninth tergum tapering posteriorly; apicolateral processes slender, digitiform, slightly bent; pair of submedial setose lobes



Figs. **94-99.** *Culicoides (Selfia) denningi* Foote and Pratt. **94,** pupal respiratory horn; **95,** female operculum; **96,** silhouette of opercular teeth; **97,** last abdominal segment of female pupa; **98,** last abdominal segment of male; **99,** larval epipharynx.

on posterior margin. Ninth sternum slightly emarginate, bearing two caudally projecting, contiguous lobes on posteromesal edge, lobes seldom if ever reaching beyond level of anterolateral corner of basimere. Basimere oblong, densely setigerous, with numerous long heavy setae on inner face; narrow strip at anterior end of basimere heavily sclerotized, mesal edge protruded and articulating with swelling on lateral edge of arm of aedeagus; basimeric root elongate, truncate, without hook-like process on posterior margin. Telomere basally stout, narrowing to rather knobbed apex. Aedeagus with two posteriorly bent sclerites forming a more or less Y-shaped structure; median posterior portion short, with a pair of indistinct,

subapical, inner rod-shaped structures, most conspicuous in uneverted state; anterior aedeagal "arms" slender, strongly divergent; arms dark anteriorly, gradually becoming lighter posteriorly. Claspettes fused (Fig. 85); median posterior process short, rounded, bordered basally by large, prominent, squared cornered shoulders; anterior processes thin, straight, with high mesal arch.

PUPA: Light brown, sometimes yellowish brown. Quantitative characters summarized in Table 3.

Respiratory horn (Fig. 94): Arising from distinct pedicel, containing single trachea. Apex very dark, slightly wider than remainder of horn. Lateral spiracular openings and base of horn slightly darker than remainder; two, rarely three spiracular openings on prominent, unarmed protuberances. Lateral convolutions prominent above last lateral spiracular opening.

Operculum (Figs. 95-96): Brownish; opercular teeth darker, covering most of operculum in females, slightly less so in males; no striking demarcation in distribution of differently shaped opercular teeth although stronger teeth generally more abundant toward sides of operculum; teeth extending between *am* tubercles to approximately level of tip of *am* spines; *am* tubercles and spines well developed.

Cephalic-thoracic chaetotaxy: Proximal portion of antennal pad and *ad* tubercle brown, antennal pad becoming lighter distally; ventral region of head very light yellowish. Except for *ad*, cephalic and thoracic tubercles rounded. Spine of d_1 not overlapping tubercle of d_2 (Fig. 105); d_3 well removed from d_1 and d_2 and bearing short spine. Tubercle *dl* with two spines (Fig. 103), one long, filamentous, the other short, stouter. Tubercle *ad* with large strong spine and smaller, more slender one. Two pairs *vm* spines with contiguous sockets. Two pairs *vl* spines (Fig. 100).

Abdomen: All *lpm* tubercles on segments 3 or 4-8 generally with bases spiniform (Fig. 101); *lasm* tubercle with base spiniform on segments 3 or 4-7 (Fig. 107); *dpm* tubercles without spines on segments 3 and 4 (Fig. 104); *vpm* and *dasm* tubercles as in Figures 102, 106. Anal segment of female with anterior ventral band of spicules becoming very sparse or absent at lateral margins (Fig. 97); male with broad band of spicules (Fig. 98); genital sheaths prominent, contiguous; mesal lobe arising just anterior to base of sheaths with small pore or protuberance at apex. (In some specimens it is open and resembles a pore, while in others it appears to be a finger-like projection.) Posterolateral process of both sexes strongly divergent, distal portions very dark.

LARVA: Head length of fourth instar larva 157μ (150-162, $\pm$4.9; n=13); width 105μ (91-117, $\pm$7.4; n=13); width of oral ring 66μ (58-72, $\pm$4.7; n=13). Ratio of head width to breadth 1.5 (1.33-1.60; n=13). For chaetotaxy see Figures 10, 12 and 13 and section on Morphology.

Figs. **100-107.** *Culicoides (Selfia) denningi* Foote and Pratt. **100,** *vm* and *vl* setae; **101,** lpm tubercles; **102,** *vpm* tubercles; **103,** *dl* tubercle; **104,** *dpm* tubercles; **105,** *d* tubercles; **106,** *dasm* tubercles; **107,** *last* tubercle.

Epipharynx (Fig. 99): Well sclerotized. Lateral arms stout; fringe of hairs arising from shoulder region; dorsal comb with nine sharp teeth; frontal comb with five low, rounded teeth.

TYPE: The holotype of *denningi* is in the USNM collections.

Specimens examined:

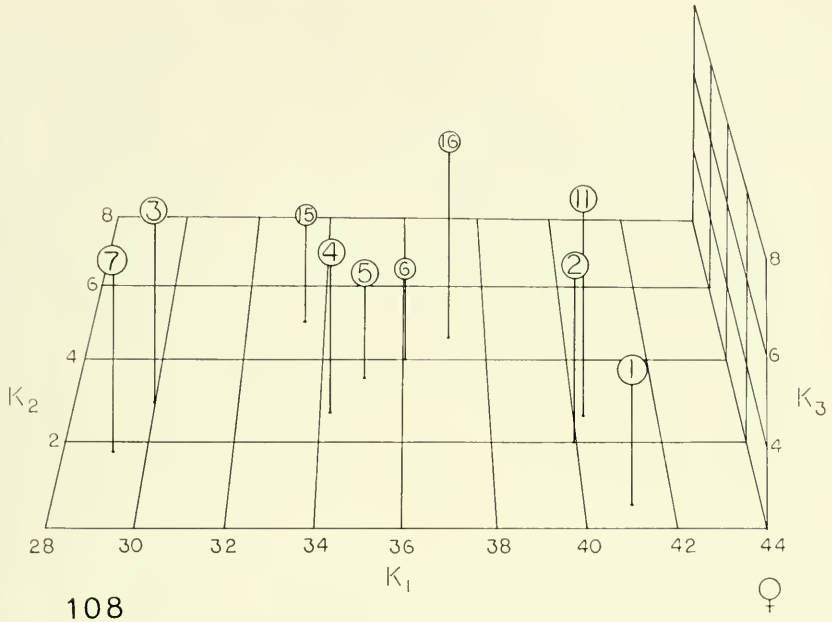
COLORADO: Larimer County, Ft. Collins, 1 Aug. 1942, light, M. A. Palmer, 4 males, 5 females. MONTANA: Big Horn County, 12 mi. S. Custer, 2700 ft., 8 Aug. 1968, reared, 3 females, each with associated pupal skins. Custer County, Pumpkin Ck., 30 mi. N. Volborg, 2400 ft., 8 Aug. 1968, reared, 2 males, 1 female, each with associated pupal skin. Miles City, 7 Sept. 1962, light, 1 female. Yellowstone County, Billings, reared, 4 females. NEBRASKA: Scotts Bluff County, Mitchell, 2 Nov. 1953, light, 1 female. Sheridan County, Hay Spring, 18 July 1944, light, 1 male. NEVADA: Elko County, Salmon Falls Ck., 2 mi. S. Jackpot, 4900 ft., 30 July 1968, reared, 1 male, 5 females, each with associated pupal skin. N. Fork Humbolt River, 16 mi. N. E. Elko, 5200 ft., reared, 4 males, 8 females, each with associated pupal skin. Hendricks Ck., S. E. Mountain City, 6200 ft., 30 July 1968, reared, 1 male with associated pupal skin. Humbolt County, Winnemuca, 16 June 1952, 1 male, 4 females. Lauder County, 5 mi. E. S. E. Austin, 6750 ft., 5 Aug. 1964, 1 male. White Pines County, 5 mi. W. Baker, 7000 ft., 4 Aug. 1964, 1 male. OREGON: Malheur County, 5 mi. W. Vale, 9 Aug. 1961, light, 2 males, 8 females. Little Valley, S. W. Vale, 19 June 1963, light, 1 male, 6 females. 12 mi. S. Adrian, 21 Sept. 1967, light, 2 females. Ontario, 28 Aug. 1962, light, 1 female. SOUTH DAKOTA: Fall River County, Oral, 4 July 1953, 2 males. UTAH: Cache County, Logan, 1 July 1957, light, 2 males, 2 females. Duchesne County, Roosevelt, 17 July 1952, 1 male. Garfield County, Sevier River at U.S. #18 and #89, 7100 ft., 20 July 1968, reared, 4 males, 3 females, each with associated pupal skin. E. Fork Sevier River, 3 mi. W. Ruby's Inn, 7700 ft., 20 July 1968, reared, 3 males, 3 females, each with associated pupal skin. Grand County, Hartley Dome, 13 Aug. 1958, 2 males, 2 females. Green River State Park, 12 July 1968, light, 3 males. Juab County, Sevier River, 20 mi. S. W. Nephi, 4800 ft., 24 July 1968, reared, 8 males, 8 females, each with associated pupal skin. Millard County, Delta, 4670 ft., 24 July 1968, reared, 5 males, 2 females, each with associated pupal skin. Uintah County, Green River, Dinosaur Nat'l. Mont., 4500 ft., 9 July 1968, reared, 14 males, 14 females. WASHINGTON: Adams County, Othello, 4-30 July 1967, 7 males. Grant County, O'Sullivan Dam, July 1955, 4 males, 1 female. Ephrata, Lower Crab Ck., 4 Sept. 1960, 2 males. WYOMING: Poison Water Ck., 1 mi. S. W. Shoshoni, 4800 ft., 7 July 1968, reared, 2 females, each with associated pupal skin. Park County, Big Sand Coulee, 13 mi. S. Belfry, 4000 ft., 7 Aug. 1968, W. R. Atchley, reared, 6 males, 7 females, each with associated pupal skin. Platte County, Burnett Ranch, 1 July 1965, 4 males. Brown Ranch, 1 Aug. 1967, 1 male. Sublette County, Cottonwood Ck., 10 mi. S. Daniel, 7000 ft., 8 July 1968, reared, 1 female with associated pupal skin. Sweetwater County, Rock Springs, 28 July 1940, 1 male, 1 female.

CANADA: Alberta, Lethbridge, 17-31 July 1955, light, 2 males, 2 females. Saskatchewan, Saskatoon, Aug. 1947, R. Coleman, light, 8 females, PARATYPES. Saskatoon, South Saskatoon River, 5-11 Aug. 1960, reared, 10 males, 20 females, 25 larvae, 35 pupae. Saskatoon, 19-20 Aug. 1957, light, 4 males, 5 females.

Statistical Analysis of Variation

Analysis of variance of the 10 male characters indicate significant variation at the $P<.001$ level in all except the width of the telomere apex which is significant at $P<.01$ and the number of antennal sensory pits which is not significant. In the females, variation in the number of antennal sensory pits was significant at $P<.05$ while the remaining 15 characters were significant at $P<.001$.

Means for *denningi* characters by locality are given in Tables 4, 5 and 6. Pooled within locality variance-covariance matrices are given in Tables 7 and 8. Partition of roots in the discriminant matrix of 10 measurements on males gave a total variance of 560.238. The first component accounted for 85.17% of the variance, while K_2 and K_3 together accounted for only 10.24%.



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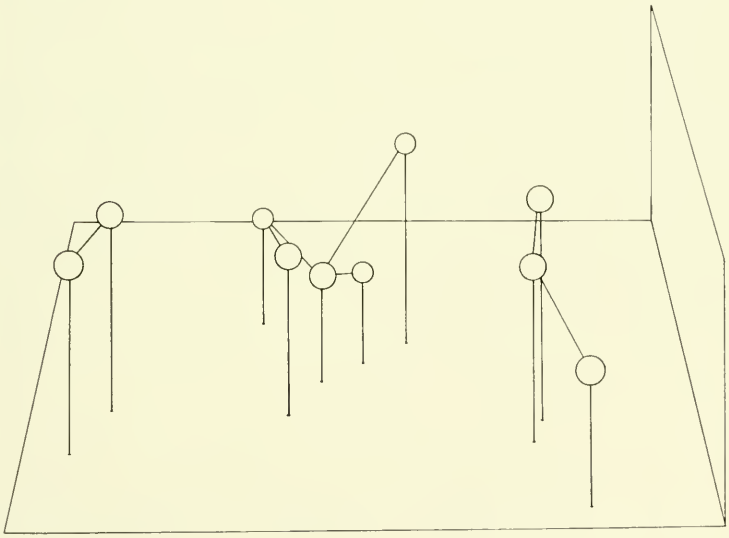

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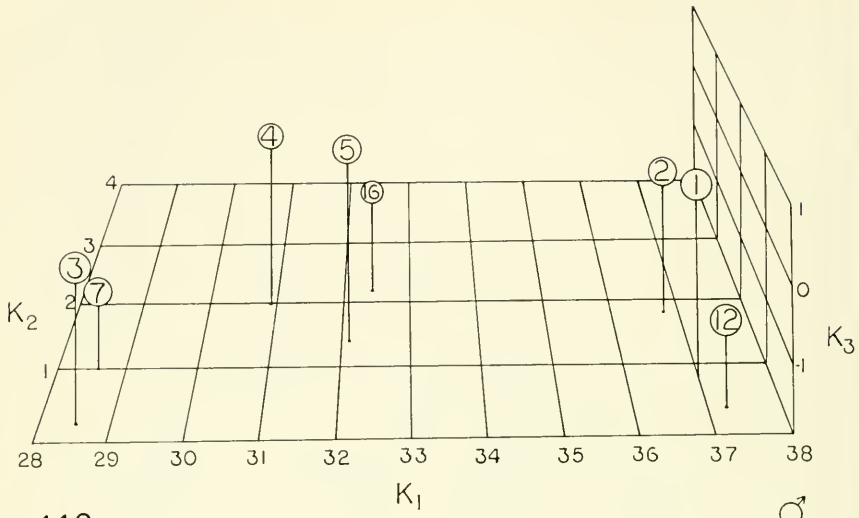
Fig. **108.** Projection of means of 10 samples of *C. (S.) denningi* females onto the first three discriminant functions. The size of the balls implies distance from the viewer. For explanation of locality codes, see Table 4. Fig. **109.** Samples of *C. (S.) denningi,* as shown in Figure 108, linked by the lowest value between pairs of samples in a generalized distance matrix.



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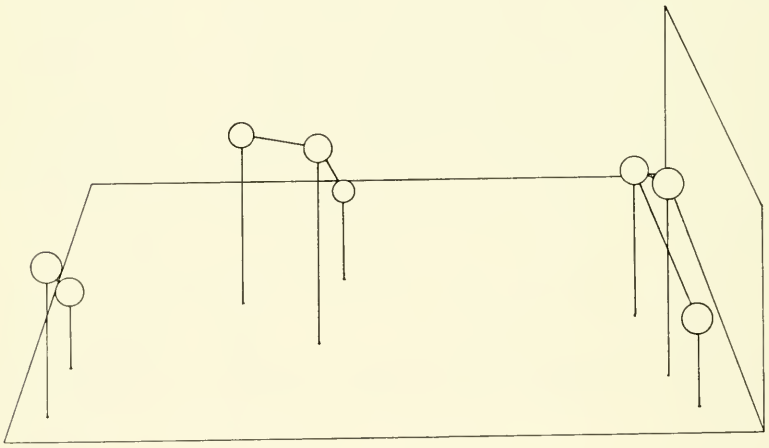

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FIG. 110. Projection of means of eight samples of *C. (S.) denningi* males onto the first three discriminant functions. The size of balls implies distance from the viewer. For explanation of locality codes, see Table 4. FIG. 111. Samples of *C. (S.) denningi,* as shown in Fig. 110, linked by the lowest value between pairs of samples in a generalized distance matrix.

The first five components were high significant ($p<0.001$), the sixth at $p<0.05$, and the seventh was not significant. In females the total variance was 1221.642, of which K_1 explained 75.94% and K_2 and K_3 together 13.86%. All nine components were highly significant.

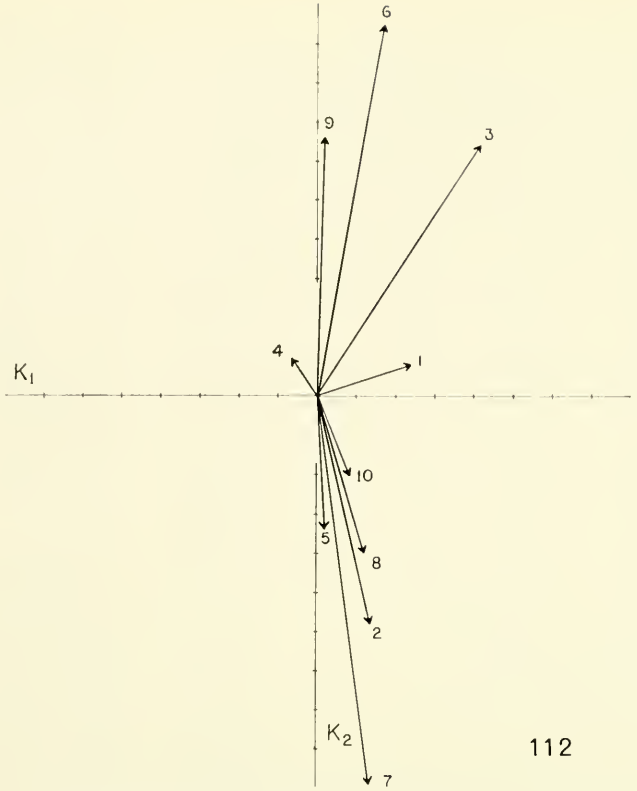
The projection of the group means of 11 localities onto discriminant functions (Figs. 108-111) and the results of the simultaneous testing procedure indicate three homogenous groups. In the females samples 3 and 7 and 1, 2 and 11 were significantly different from 4, 5, 6, 15 and 16 at the 0.025 level. In males, 1, 2 and 12 were significantly different from 4, 5 and 16 at the 0.005 level, but 3 and 7 were not significantly different from the intermediate group composed of 4, 5 and 16.

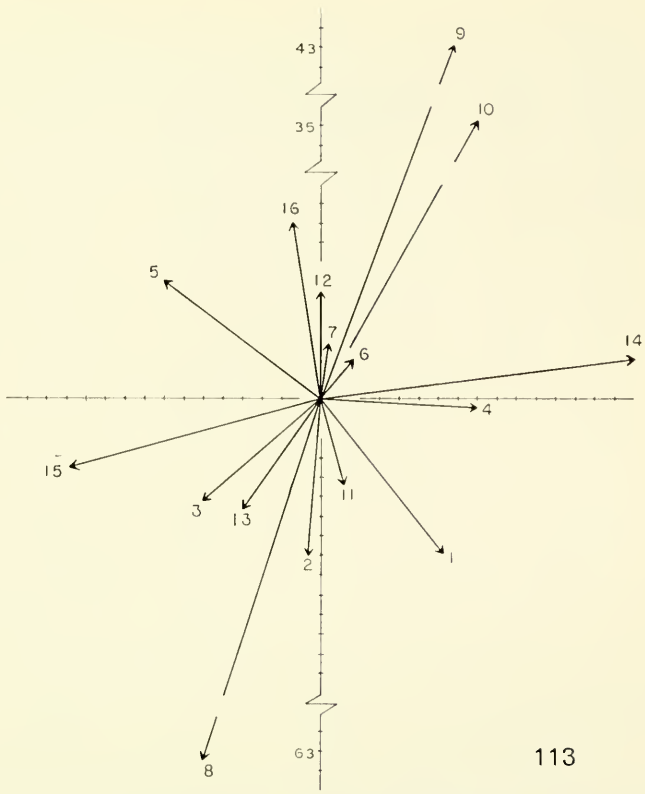
The set of vectors (Figs. 112-113), plotted for the first two discriminant functions, shows the trends in geographic variation when compared to Figures 108 and 110. This analysis indicates the major trend in geographic variation in *denningi* to be one of size. Individuals from localities with greater values for K_1 are generally larger with longer hind legs, longer and broader wings, and more elongate third palpal segment. In addition, the females with higher K_1 values generally have more maxillary teeth and a more elongate head and proboscis. Localities 3 and 7 contain very small individuals, 1, 2 and 12 very large individuals, and the middle cluster is intermediate in size.

Those localities with higher K_1 values are for the most part either from very high elevations in the southern part of the range, as in the Garfield County, Utah, samples, or from more northern latitudes. Two exceptions to this include the Saskatoon, Saskatchewan, and Big Horn County, Montana, samples, which are found in the intermediate group. As will be shown later, the latter locality is in a hybrid zone and, therefore, little reliance can be placed on its position.

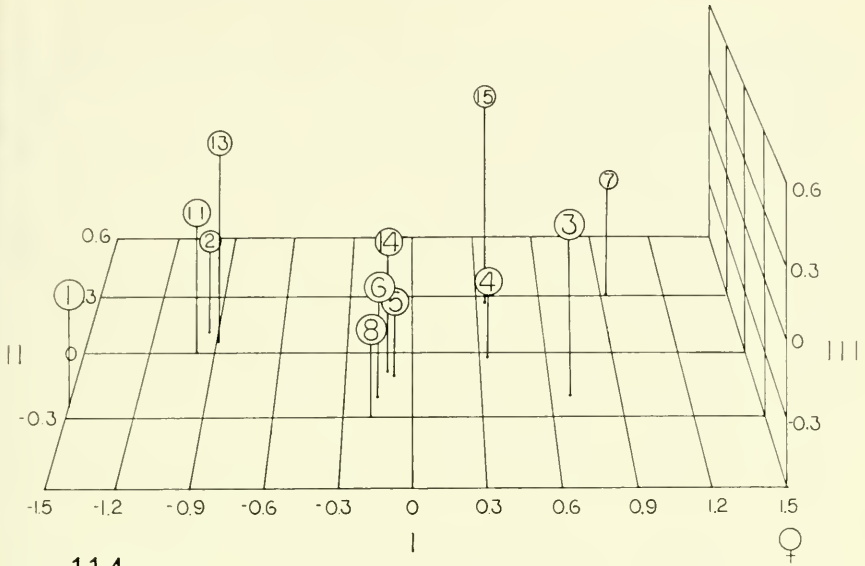
With the exception of the Canadian sample, variation in this species would seem to follow Bergmann's ecogeographical rule, which states that body size in geographically variable species of warm blooded vertebrates tends to be larger in cooler parts of the range. As pointed out by Mayr (1963), the correlation between body size and conservation of body heat has no validity in poikilothermic animals. Rather, in these organisms body size may be determined by the length of the available growing period, presence or absence of competition, humidity, or other factors. Similar increases in size of certain body parts with changes in latitude or elevation have been reported by several authors, including Rensch (1943), Alpatov (1929), etc. Further, geographic variation in *C. hieroglyphicus* and *jamesi* shows similar patterns, but not to the degree seen in *denningi*.

The extensive size variation in *denningi* is demonstrated by comparing the two localities with low K_1 values (Juab County, Utah, and Elko County, Nevada) with the three samples with high K_1 values (Garfield County, Utah, and Park County, Wyoming). The wing, flagellum, head, hind femur and third maxillary palpal segment are about 1.4 times as long in the latter samples as in the former. Some of the body parts apparently





FIGS. **112-113.** Vectors for 10 characters of males and 16 characters of females of *C. (S.) denningi* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would generate if it varied independently. For explanation of character codes, see text.



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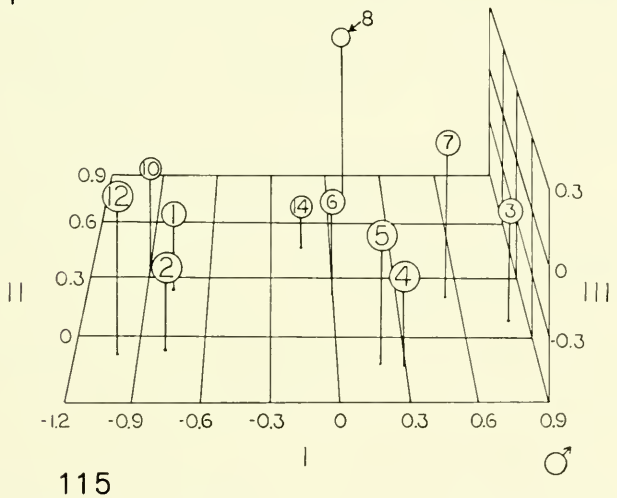

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Figs. **114-115.** First three principal components of 12 samples (11 in females) of *C. (S.) denningi*.

do not grow harmonically in the various regions of the body. For example, the palpal ratio (length of third maxillary palpal segment divided by greatest breadth) is about 2.7 for the samples with high K_1 but 2.3 for those with low K_1. Such a steep cline would indicate considerable restriction in gene flow among these populations.

Geographic variation patterns in the pupae of *denningi* are described in Atchley (1970).

The first principal component in the females plotted in Figure 114 explained 54.80% of the variance, while II and III together accounted for 13.71%. A total of eight factors were extracted, which had an accumulated value of 85.89%. The first component in females is, as in the other species, a "general body size" factor with high loadings for the length of the hind leg segments, wing and various parts of the flagellum. The second component is an "*lpm* tubercle" factor with high values for number of spiniform and semi-spiniform tubercles on abdominal segment eight in pupa, while III is a "horn color" factor. The remaining factors had loadings as follows: IV, number of lateral spiracular openings on the respiratory horn; V, color of the pupal abdominal skin; VI, number of tibial spines on the hind leg; VII, number of multiple antennal sensory pits; and VIII, number of antennal sensory pits.

In males (Fig. 115), factors I-III explained 59.53% of the variance, while the total of nine accounted for 83.70%. Factor I is again a "general body size" factor with greatest weight on the length of the hind femur, tibia and basitarsus, while II is a "d_2" factor and III an "*lpm* tubercle" factor. The remaining factors and their loadings are as follows: IV, color of the respiratory horn and abdominal skin; V, number of lateral spiracular openings on the horn; VI, width of the horn tip; VII, number of tibial spines on the hind leg; VIII, number of antennal sensory pits; and IX, the length of spine d_3 in the pupa.

Culicoides (Selfia) hieroglyphicus Malloch

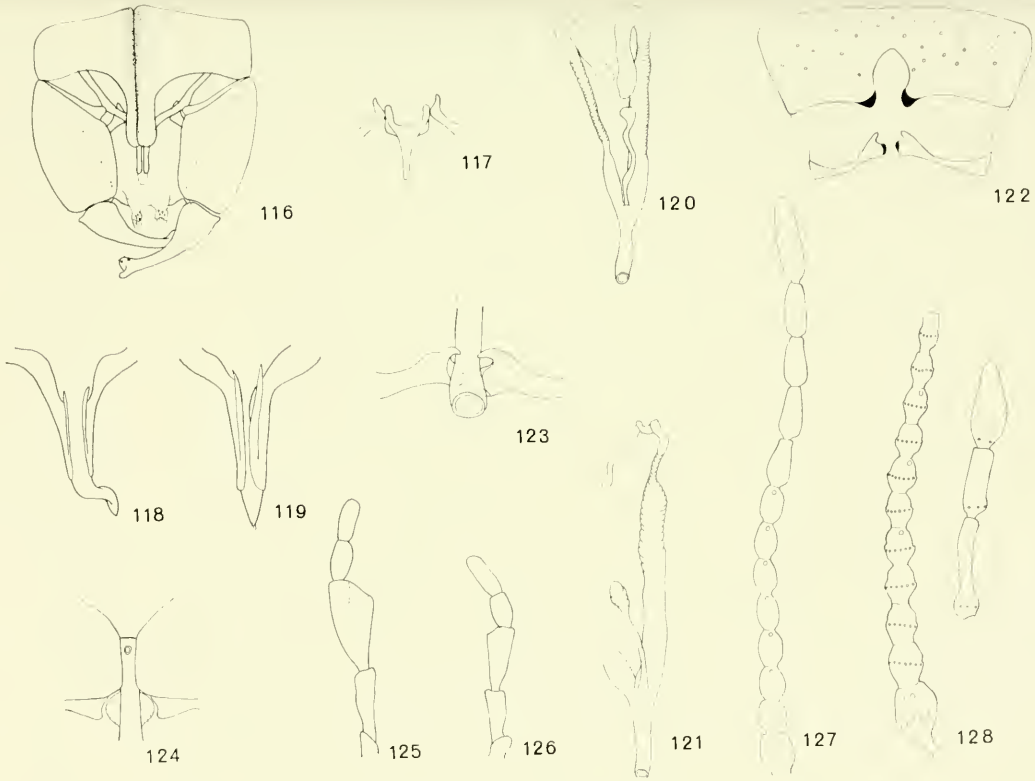
(Figs. 4-7, 9, 116-148)

Culicoides hieroglyphicus Malloch, 1915, Ill. State Lab. Nat. Hist. Bull. 10:297 (female; Ash Creek, Graham Mt., Arizona; fig. mesonotal disc).
Culicoides (Selfia) hieroglyphicus; Khalaf, 1954, 38.

The following description is based on about 60 specimens, most of which were reared from larvae or pupae from the Pecos River, east of Roswell, New Mexico.

FEMALE—Length of wing 1.14 mm (1.08-1.20, ±0.03; n=15); width 0.56 mm (0.53-0.58, ±0.02; n=15).

Head: Vertex with numerous long setae. Eyes close together, separation 0.15-0.35 as wide as long (Fig. 124). Antennal flagellomeres in proportion of 13:9:10:10:10:10:10:10:13:14:14:15:25; proximal eight flagellomeres roughly 1.4 times as long as broad (Fig. 127); total length of flagellum 484μ (456-505, ±15.0; n=15); antennal ratio 1.03 (0.94-1.14; n=15); antennomeres 9+10 to 11 in ratio of 0.65 (0.60-0.72; n=15); distal sensory pits on antennomeres 3, 5-10, occasionally on 4 or absent from 5; occasionally 1-2 multiple sensory pits present on antennomeres other than 3. Distal four palpal segments in proportion of 15:25:10:13; third segment moderately swollen, 2.1 (1.9-2.5; n=15) times as long as greatest breadth, with a deep



Figs. **116-128.** *Culicoides (Selfia) hieroglyphicus* Malloch. **116,** male genitalia, claspettes removed; **117,** claspettes; **118,** apex of aedeagus showing everted state; **119,** uneverted state; **120,** spermathecae; **121,** abnormal type of spermathecae; **122,** abdominal sterna eight and nine of female; **123,** ninth sternum supporting bursa; **124,** female eye separation; **125,** female palpus; **126,** male palpus; **127,** female flagellum; **128,** male flagellum.

sensory organ (Fig. 125). Total length of head 351μ (332-372, $\pm$12.2; n=15); ratio of head length to proboscis 1.19 (1.13-1.28; n=15). Mandibles with 12 (11-14; n=15) teeth. Maxillae with 16 (14.17; n=15) teeth.

Thorax: Mesonotum dark brownish black with grayish markings; median brown band bordered by pair of narrow gray stripes; gray stripes broken twice by transverse connections from median stripe and bounded along mesal third by large patch of brown; small, often rather faint brownish band extending laterally from humeral pit; pit bordered posteriorly and laterally by grayish patches; prescutellar area grayish. Legs light brown to brown, femorotibial joint slightly darker. Fore legs with subbasal femoral and preapical tibial pale bands; middle legs generally unicolorous but occasionally with very faint preapical tibial band; hind leg with faint preapical tibial band. In dark specimens basal portions of femur, trochanter and coxa lighter and tarsi often slightly paler. Hind leg with segments in proportion of 55:26:134:131:72:31:20:13:15; hind tibial comb with four spines, occasionally one leg with five, basal four hind tarsomeres with distal spine. Scutellum with one pair median and one pair lateral macrosetae; one microseta outside each lateral macroseta, 2-4 microsetae between median and lateral macrosetae. Stigma of wing brownish. Macrotrichia abundant over practically entire wing, most dense in anterior part of cell R_{5}. Costa extending 0.56 (0.53-0.57; n=15) of entire wing length.

Abdomen: Light brown to brown. Eighth sternum with moderately deep pocket; postero-lateral edges of pocket lacking hook-like processes (Fig. 122); ninth sternum divided, with prominent, anteriorly directed mesal thumb-like lobes. Spermathecae three (Fig. 120), very lightly sclerotized; outer two very long (260μ and 273μ), extending into sixth segment, usually bent back posteriorly or coiled (if straight, would project into fifth segment); apical end with unusual, rather obscure patterning; apical portion often markedly narrowed (Fig. 121) but usually difficult to see in its entirety due to very light sclerotization. Third spermatheca shorter, more slender, distally bulbous, 104μ long.

MALE—Length of wing 0.94 mm (0.91-1.0, $\pm$0.03; n=12); width 0.40 mm (0.36-0.42, $\pm$0.02; n=12).

Head: Brown; appendages usually slightly paler, distal three flagellomeres darker than preceding ten. Antennal flagellomeres in proportion of 17:10:10:10:10:10:10:10:10:11:28:20:25 (Fig. 128); distal sensory pits on antennomeres 3, 8 and 10, often on 6; flagellar length 55μ (539-577, $\pm$11.2; n=12). Distal four palpal segments in proportion of 11:18:9:12; third segment slightly swollen, with small, deep sensory organ (Fig. 126). Head length 328μ (294-341, $\pm$15.3; n=10).

Thorax: Leg coloration as in females. Hind leg with segments in proportion of 45:23:122:119:63:29:18:12:15; hind tibial comb with four

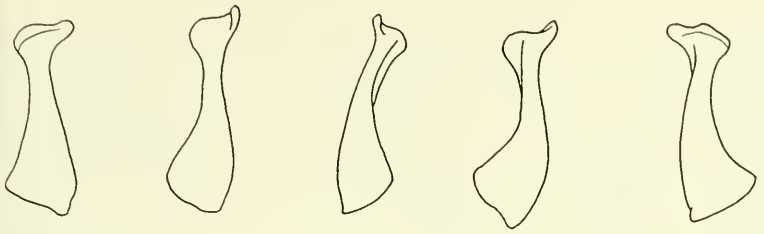


Fig. 129. Variation in apex of telomere in *Culicoides (Selfia) hieroglyphicus*.

spines, rarely five on one leg. Scutellum with one pair median and one pair lateral macrosetae; a single microseta between median and lateral macrosetae. Stigma pale grayish brown; macrotrichia abundant in anterior part of wing, sparse in other cells, absent in vannal cell. Costa extending 0.48 (0.46-0.50; n=12) of entire wing length.

Genitalia (Figs. 116-117): Ninth tergum strongly tapering caudally, with very slender, divergent apicolateral processes; a pair of prominent subapical setigerous lobes on postero-median margin. Ninth sternum with long, posteriorly projecting, contiguous processes, the separation between lobes continuing anteriorly, apparently dividing sternum (Fig. 116), dividing line bordered by paler membranous area; processes extending posteriorly to level of anteriormost corner of arm of basimeric root. Basimere short, longer than broad, with numerous long setae, particularly conflect on inner face; single, postero-laterally directed, long, apically flattened root; cephalic end of basimere heavily sclerotized, with protruding knob-like mesal corner which articulates with lateral swelling on aedeagal arm. Telomere basally stout; apex foot-shaped and often faintly concave; toe portion usually curved but variable (Fig. 129). Aedeagus with two slender, slightly sinuate, heavily sclerotized pieces; in uneverted state (Fig. 119), pair of elongate rods rather prominent on inner margins of posterior end; as aedeagus becomes more everted, rods appear less distinct (Fig. 118); arms slightly arcuate with small, lateral swelling attingent to sclerotized antero-mesal corner of basimere. Claspettes fused (Fig. 117), long, attenuate, with small lateral shoulders; anterior processes short.

PUPA: Quantitative characters summarized in Table 9.

Respiratory horn (Fig. 130): Arising from prominent pedicel, containing a single trachea. Apex very dark, remainder pale yellow to yellow, except generally light brown spiracular protuberances; apex same as, or slightly wider than, remainder of horn. Two, rarely three, lateral spiracular openings on unarmed, widely separated protuberances. Lateral convolutions prominent above last spiracular opening, lacking below.

Operculum (Figs. 131-132): Brown; teeth slightly darker. Larger opercular teeth generally confined to outer one-third, sometimes to outer one or

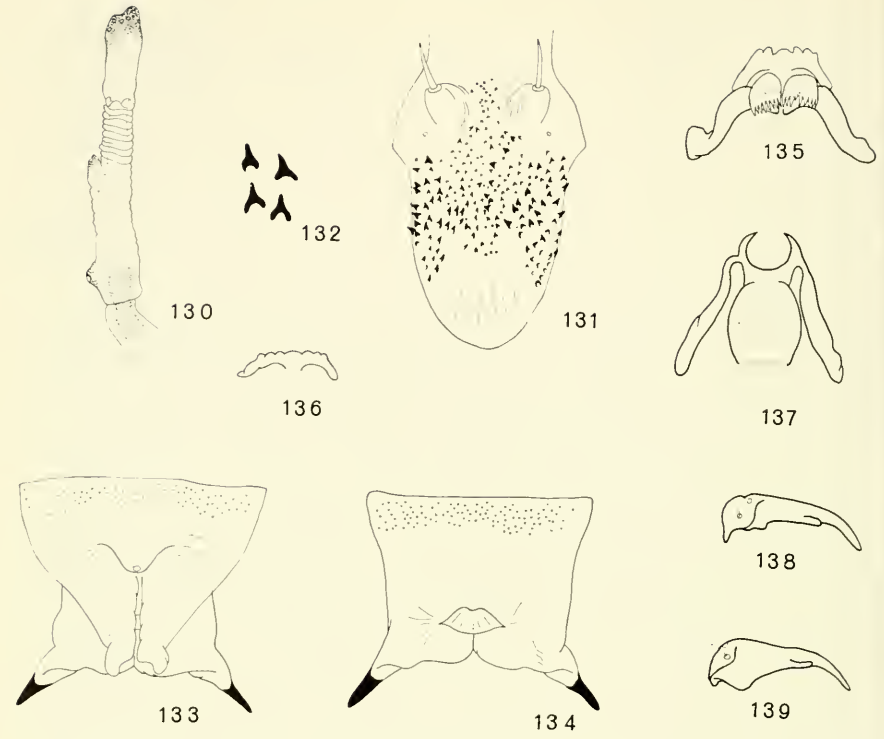
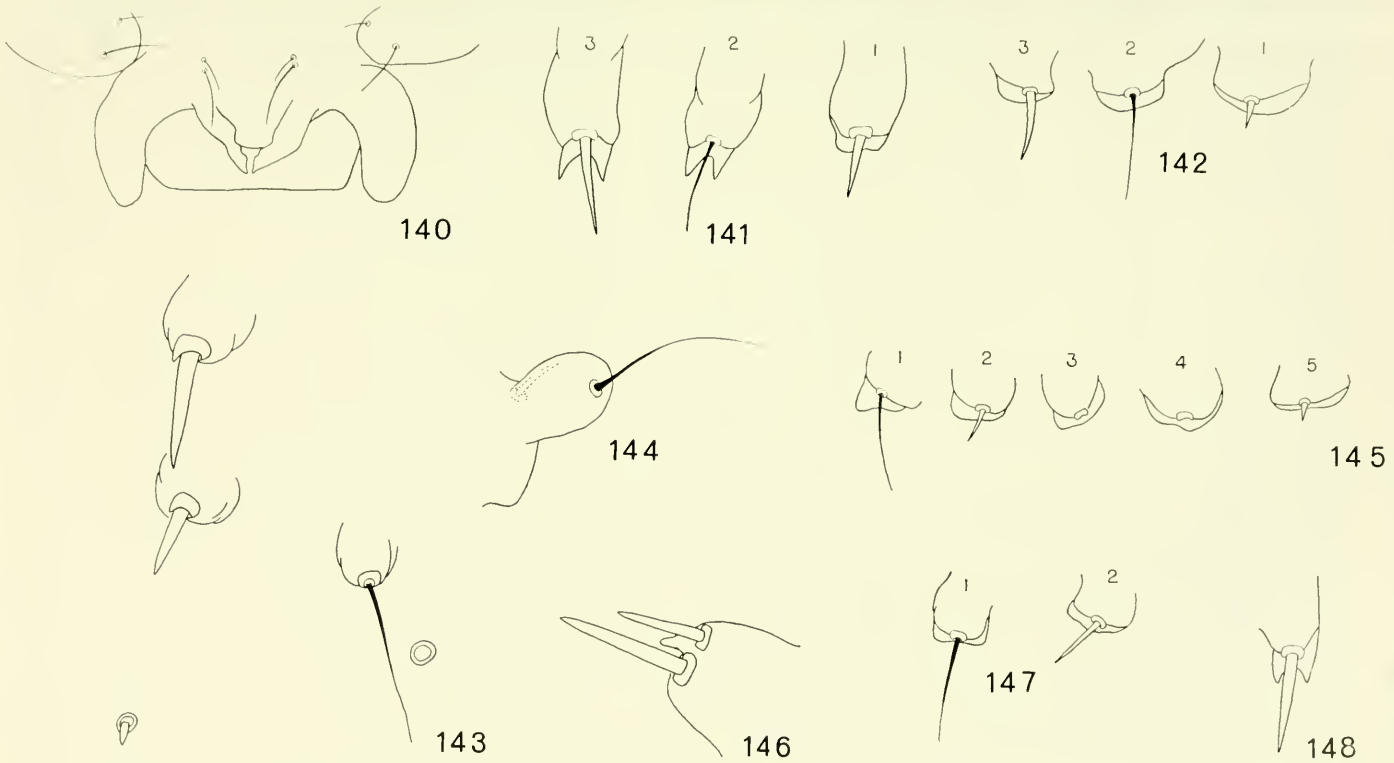


FIG. 130-139. *Culicoides (Selfia) hieroglyphicus* Malloch. **130,** pupal respiratory horn; **131,** female operculum; **132,** silhouette of opercular teeth; **133,** last abdominal segment of male pupa; **134,** last abdominal segment of female; **135,** epipharynx of male larva; **136,** frontal comb of epipharynx of female; **137,** hypopharynx; **138,** larval mandible of male; **139,** larval mandible of female.

two rows; extending posteriorly between *am* tubercles to level of posterior margin of tubercle; *am* tubercles and spines well developed.

Cephalic-thoracic chaetotaxy: Base of antennal pad and *ad* tubercle dark, antennal pad lighter distally; ventral region of head yellowish. With exception of *ad* (Fig. 146) and occasionally d_1, cephalic and thoracic tubercles rounded. Spine of d_1 usually overlaps tubercle of d_2 (Fig. 143), d_3 spine small, well separated from d_2. Two pairs *vl* and two pairs *vm* spines (Fig. 140). Tubercle *dl* as in Figure 144.

Abdomen: lpm tubercles with bases generally spiniform on eighth segment only (Fig. 141), occasionally seventh or sixth may bear spiniform tubercles, but more often these are semi-spined; also, not all tubercles on eighth spiniform, some may be semi-spined or even rounded; *lasm* tubercle spiniform on more posterior segments (Fig. 148); *dpm* tubercles 3 and 4 lacking spines (Fig. 145); *vpm's* as in Figure 142; *dasm's* as in Figure 147.



Figs. **140-148.** *Culicoides (Selfia) hieroglyphicus* Malloch. **140,** *vm* and *vl* setae; **141,** *lpm* tubercles;**142,** *vpm* tubercles; **143,** *d* tubercles; **144,** *dl* tubercle; **145,** *dpm* tubercles; **146,** *ad* tubercle; **147,** *dasm* tubercles; **148,** *lasm* tubercle.

Last segment of both sexes with strongly divergent lateral processes (Figs. 133-134); anterior band of spicules appears to thin out laterally in both sexes, particularly on ventral side; genital sheaths of male with distinct apices, generally in same shape as adult telomere (Fig. 133); prominent mesal lobe at base of genital sheaths bearing small protuberance or pore at caudal end.

LARVA:

Mandible: Broad basally, with curved, pointed apex; thumb-like process appressed to inner surface of tooth; mandible of female (Fig. 139) apparently slightly broader basally than that of male (Fig. 138) (more material needed to confirm this). Mandible 46μ long (n=3).

Epipharynx: Well sclerotized. Lateral arms stout, apices directed laterally, expanded; 61μ between apices of arms; fringe of minute hairs arising from shoulder of lateral arm apparently absent on available material; dorsal comb with eight or nine long, sharp teeth; frontal comb massive, possessing six or seven rounded teeth. A male (Fig. 135) shows six teeth while the female (Fig. 136) has seven. This might be due to variation in mounting rather than sexual dimorphism, as the seventh tooth may be obscured in the male.

Hypopharynx: as in Figure 137.

TYPE: The holotype of *hieroglyphicus* is in the Illinois Natural History Survey collections.

DISTRIBUTION: This species is distributed as in Figure 83.

Specimens examined:

ARIZONA: Cochise County, St. David, Oct. 1953, light, 2 males. Graham County, Ash Ck., Graham Mt., 3200 ft., 15 June 1914, E. G. Holt, 2 females, PARATYPES. Gila River, Pima, 7 August 1967, light, 1 male. Maricopa County, Tortilla Flats, 6 August 1967, light, 11 males, 22 females. 3 mi. S. Cave Ck. P. O., June 1942, 3 males. Wickenburg, Aug. 1950, 4 males, 6 females. Pima County, Quitobaquito, 26 April 1959, 1 male. Sabino Canyon Stat., Catalina Mts., 2 March 1959, 4 males, 2 females. Sabino Canyon, N. E. Tucson, 9 Aug. 1967, reared, 2 males, 1 female, each with associated pupal skin. Yavapai County, Red Rock Crossing, 2000 ft., 5 Aug. 1967, reared, 2 males, 2 females, each with associated pupal skin. Montezuma Well Nat'l. Mont., 2 Sept. 1953, 1 male. CALIFORNIA: Kern County, Poso Ck., 23 Aug. 1966, truck trap, 1 male. 6 mi. S. E. Buttonwillow, 26 Sept. 1967, reared, 10 males, 6 females, each with associated pupal skin. San Luis Obispo County, 2 mi. N. Cuyama, 27-28 June, light, 1 male. KANSAS: Douglas County, Lawrence, Aug. 1956, 5 males, 7 females. Ellis County, Hays, 6 June 1958, 1 female. Finney County, Garden City, 26 May 1958, 1 male, 3 females. Meade County, Lake Meade, 27 June 1964, light, 50 males, 65 females. 3 mi. E. Meade State Lake, 2800 ft., 12 Aug. 1968, reared, 2 males, 2 females, each with associated pupal skin. Riley County, Manhattan, 12 May 1965, 1 male, 6 females. NEBRASKA: Scotts Bluff County, Mitchell, 2 Nov. 1953, 1 male. NEVADA: Clark County, Logandale, 25 April 1935, 3 males, 4 females. NEW MEXICO: Catron County, Gila Nat'l. Mont., 6000 ft., 14 July 1964, 3 males. Glenwood Fish Hatchery, Glenwood, 2 Aug. 1965, 490 ft., light, 20 males, 31 females. San Francisco River, 5 mi. N. Glenwood, 5000 ft., 2 Aug. 1965, light, 42 males, 36 females. Chaves County, Pecos River, E. Roswell, 11 June 1968, 3600 ft., reared, 13 males, 15 females, each with associated pupal skin. Colfax County, Eagle Nest Lake, 7 Aug. 1965, light, 1 male. Dona Ana County, Las Cruces, 2 July 1964, light, 4 males, 19 females. Da Baca County, Alamogordo Res., 19 July 1965, light, 1 male, 2 females. Eddy County, Carlsbad, Spring 1965, light, 6 males, 20 females. Guadalupe County, Bass Lake, 21 Aug. 1967, light, 1 male, 3 females. Lincoln County, Alto Reservoir, Alto, 16 June 1965, light, 1 male. Mora County, Charette Lake, 23 July 1965, light, 2 females. Rio Arriba County, Abiquiu Res., 9 Aug. 1965, light, 1 male, 4 females. Roosevelt County, Portales, 7 July 1964, light, 2 males, 2 females. Sandoval County, Jemez River, 4 Aug. 1965,

light, 15 males, 20 females. San Miguel County, Tecolote Ck., Tecolote, 6400 ft., 23 Aug. 1967, reared, 19 males, 11 females, each with associated pupal skin. Santa Fe County, Santa Fe, 25 July 1940, 1 male. Sierra County, Cuchillo Ck., N. E. Truth or Consequences, 30 July 1965, light, 1 male, 7 females. Socorro County, Bosque del Apache, 18 July 1965, light, 10 males, 11 females. SOUTH DAKOTA: Fall River County, Oral, 4 July 1953, 1 male. TEXAS: Brewster County, Big Bend Nat'l. Mont., reared, 10 males, 9 females, each with associated pupal skin. El Paso County, El Paso, 17 June 1964, light, 3 males, 2 females. Jeff Davis County, Ft. Davis, 25 June 1954, 2 males, 3 females. Kerr County, Kerrville, June 1954, light, 6 females. Maverick County, Eagle Pass, 24 March 1941, 1 male. Presidio County, Marfa, 3 females. Randall County, Palo Duro State Park, 26 Aug. 1940, 5 females, 2 males. Terrell County, Dryden, April-May 1954, 3 males, 8 females. Sanderson, 28 April 1954, 6 males, 4 females. Val Verde County, Del Rio, 13 Oct. 1953, 4 females. UTAH: Carbon County, Coal Ck., 2 mi. E. Wellington, 5300 ft., 12 July 1968, reared, 2 males, 4 females, each with associated pupal skin. Garfield County, Escalante River, 15 mi. E. Escalante, 5100 ft., 21 July 1968, reared, 4 males, 9 females, each with associated pupal skin. Grand County, 1 mi. S. W. Cisco, 4370 ft., 13 July 1968, reared, 11 males, 15 females, each with associated pupal skin. Green River State Park, 12 July 1968, light, 8 males, 11 females. Kane County, Kanab Ck., 7 mi. N. Kanab, 5200 ft., 19 July 1968, reared, 1 male with associated pupal skin. E. Fork Virgin River, Mt. Carmel, 5300 ft., 19 July 1968, reared, 11 males, 9 females, each with associated pupal skin. San Juan County, San Juan River, Bluff, 4500 ft., 14 July 1968, reared, 12 males, 13 females, each with associated pupal skin. Uintah County, Dinosaur Nat'l. Mont., Split Mt., 22 Aug. 1965, light, 30 males, 33 females. Washington County, St. George, 17 July 1956, light, 7 females. Wayne County, Fremont River, Hanksville, 4200 ft., 23 July 1968, reared, 3 males, each with associated pupal skin. Fremont River, 15 mi. W. Hanksville, 4600 ft., 23 July 1968, reared, 4 males, 1 female, each with associated pupal skin. Fremont River, E. Capitol Reef Nat'l. Mont., 5500 ft., 10 males, 8 females, each with associated pupal skin. WYOMING: Hot Springs County, Thermopolis, 4320 ft., 1 male, 1 female. Platte County, Brown Ranch, 1 Aug. 1965, 2 males. Burnett Ranch, 1 July 1965, 1 male.

MEXICO: Sonora, Hermosillo, 12 Aug. 1959, 12 males, 12 females. Agua Caliente, 25 Aug. 1954, 1 male. Baja California, 25 mi. N. W. Penjamo, 29 Aug. 1959, 1 female.

Erroneous Records:

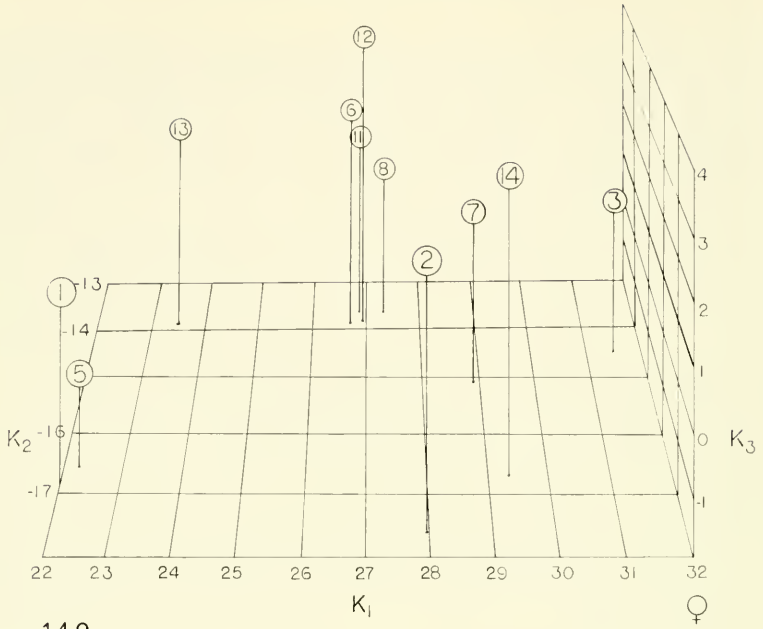
Glacier Nat'l. Park, Montana, 7000 ft. (Root and Hoffman, 1937; Foote and Pratt, 1954; Fox, 1955).

Statistical Analysis of Variation

Analysis of variance of 10 male characters indicates significant interpopulational variation in all characters at the $P<.001$ level except for the number of antennal sensory pits and the width of the telomere apex which are significant at $P<.01$. In the females, variation in the number of maxillary teeth was significant at $P<.05$ while the remaining 15 characters were significant at $P<.001$.

Character means for various populations of *hieroglyphicus* are given in Tables 10-12. Pooled within locality variance-covariance matrices are found in Tables 13 and 14. Partition of the roots in the discriminant matrix of 10 measurements from males gave a total variance of 476.464. The first three components accounted for 86.17% of the variance (among localities relative to that within localities) and the first nine components were highly significant ($p<0.001$). In females, the discriminant matrix of 16 characters gave a total variance of 1199.925, and the first three components accounted for 87.95% of the variance. The first 10 components were also highly significant.

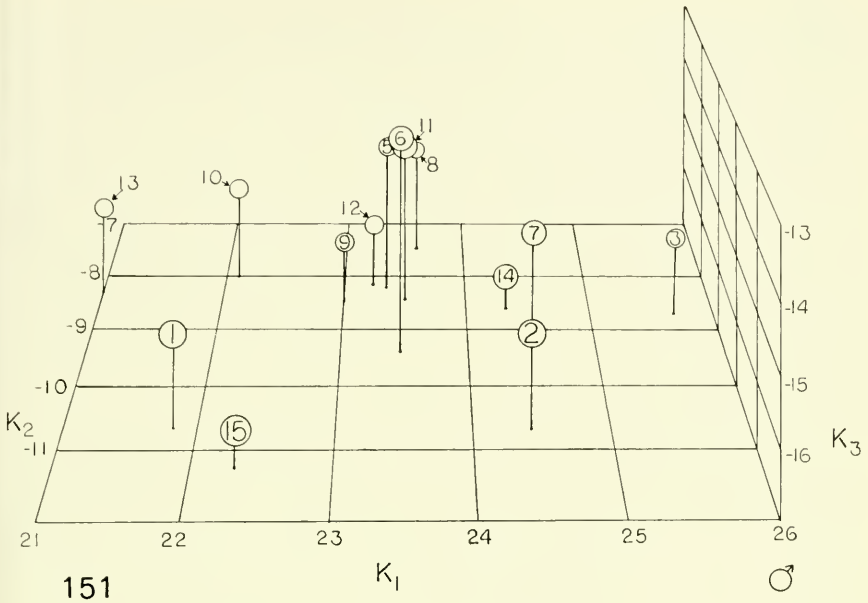
Projection of the group means of 15 localities onto discriminant functions indicates what appears to be two rather loose groups and a third more



149

150

FIG. **149.** Projection of means of 11 samples of *C. (S.) hieroglyphicus* females onto the first three discriminant functions. The size of the balls implies distance from the viewer. For explanation of locality codes, see Table 10. FIG. **150.** Samples of *C. (S.) hieroglyphicus,* as shown in Fig. 149, linked by the lowest value between pairs of samples in a generalized distance matrix.



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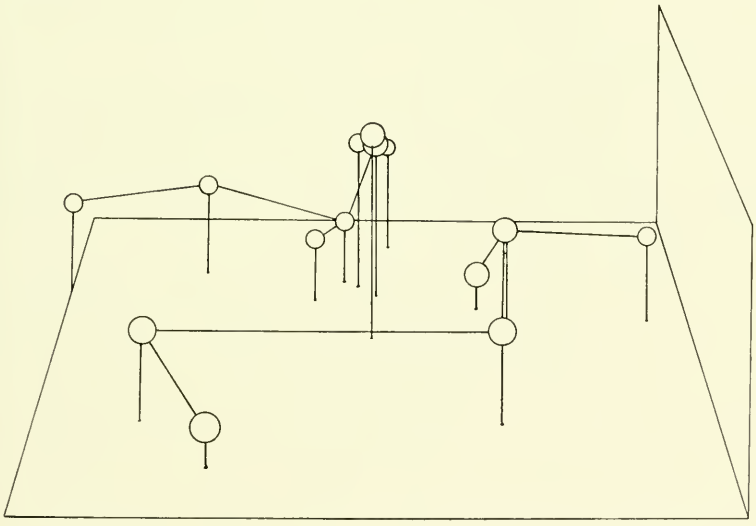


152

Fig. **151.** Projection of means of 14 samples of *C. (S.) hieroglyphicus* males onto the first three discriminant functions. The size of the balls implies distance from the viewer. For explanation of locality codes, see Table 10. Fig. **152.** Samples of *C. (S.) hieroglyphicus* as shown in Fig. 151, linked by the lowest value between pairs of samples in a generalized distance matrix.

compact one (Figs. 149, 151). With the exception of the Kern County, California, population, the compact cluster comprises localities in the Colorado River drainage of southeastern Utah. The remaining groupings would appear to make little sense on a geographic basis.

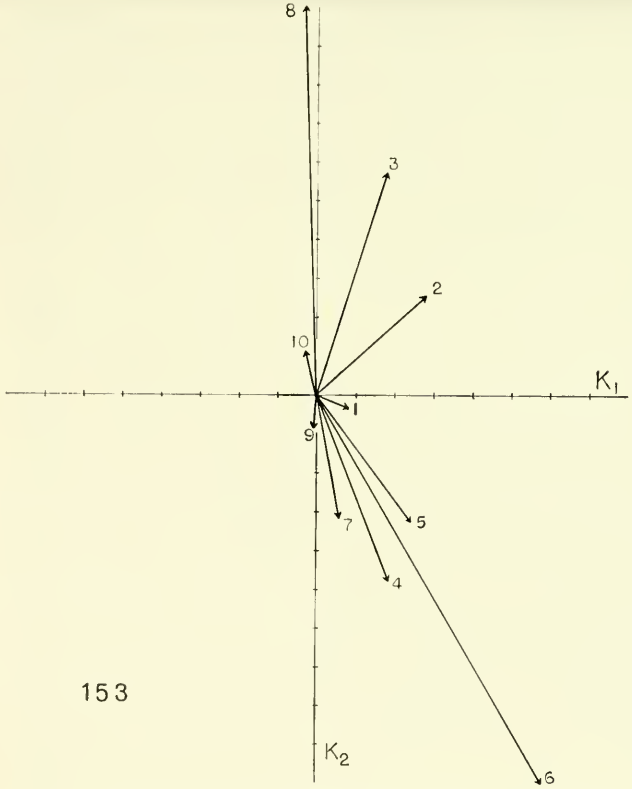
The usefulness of linking pairs of samples according to the lowest value in a generalized distance matrix is apparent when the samples of *hieroglyphicus* are examined (Figs. 150, 152). In females, the Grand County, Utah, sample, with respect to the first three discriminant functions, appears intermediate in position between samples 1 and 5 and 6, 8, 11 and 12. When the samples are linked according to their lowest generalized distance value, the Grand County sample is placed with the other southern Utah forms. In males, the Wayne and Grand County, Utah, samples are linked with the remaining southern Utah samples, while the Brewster County, Texas, flies are phenetically closer to those from Chaves County, New Mexico.

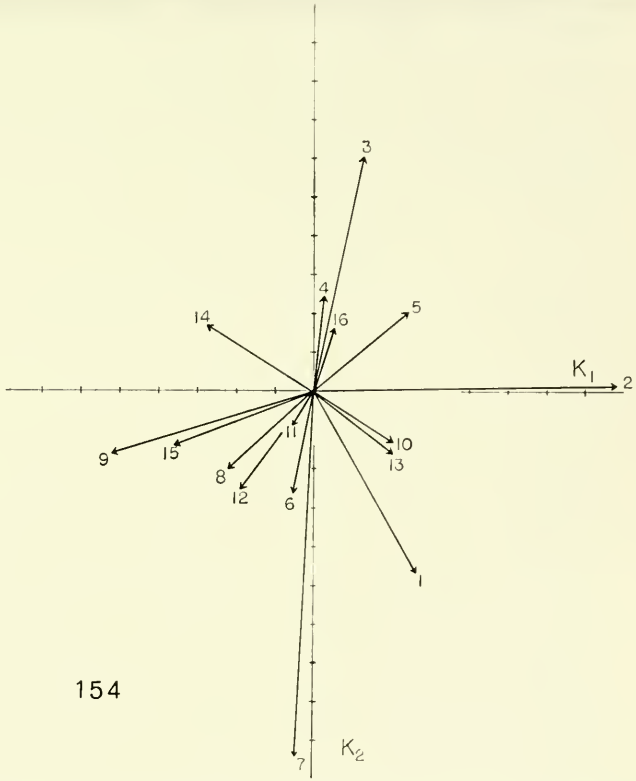
One obvious discrepancy is evident between the male and female plots. Females of the Yavapai County, Arizona, population resemble those from Brewster County, Texas, and Grand County, Utah, in that they are smaller and have more antennal sensoria, while the males are clustered with the southern Utah forms. The males of the Yavapai County sample share with the Utah forms a small number of antennal sensoria and a long wing. It should be pointed out, however, that only a few specimens of the Yavapai population were available for study.

Results of the simultaneous testing procedure showed the means of all combinations of samples were significantly different at the 0.001 level except 8 vs. 11 in females and 5 vs. 8, 5 vs. 11 and 9 vs. 12 in males. In the latter three localities, the very small sample size of localities 5 and 9 probably account for the lack of significance.

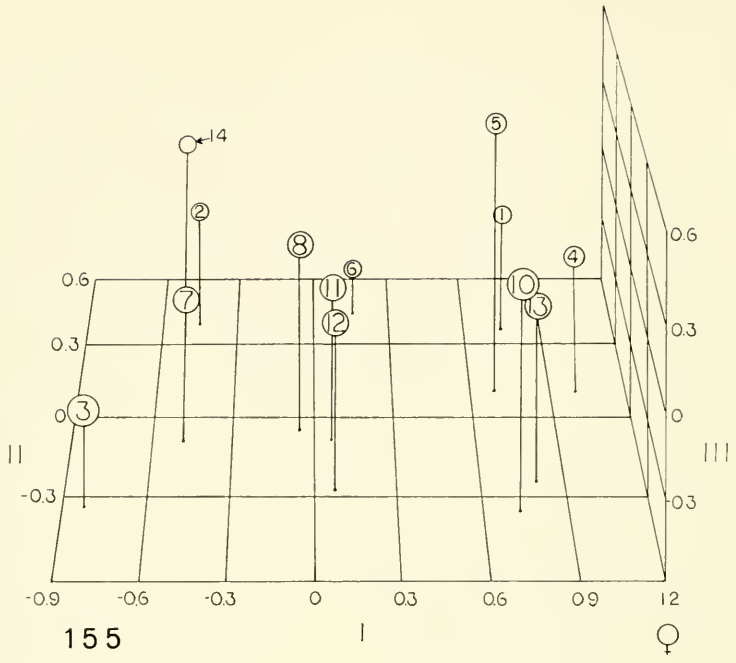
The set of vectors (Figs. 153-154), plotted for the first two discriminant functions, show the trends in geographic variation when compared to Figures 149 and 151. In both sexes, those flies from localities with low values for K_1 are generally smaller, having a shorter costa, third palpal segment and leg segments and, in addition, the females have a shorter flagellum and head. In samples with low K_2 values, the antennae have more sensoria.

In the principal components analysis, eight factors were extracted for the males, which accounted for 73.23% of the variance. The first three, plotted in Figure 156, explained 54.55%. Factor I was a "general body size" factor with highest loadings (in order of greatest contribution) for lengths of femur, tibia, wing and basitarsus. Component II was an *"lpm"* factor for the number of spiniform *lpm* tubercles on the eighth abdominal segment of the pupa and the number of abdominal segments possessing spiniform tubercles, and III could be considered a "pupal thoracic spine" factor with high loadings for the length of spine d_1 and *ad*. In males, the highest





Figs. **153-154.** Vectors for 10 characters of males and 16 characters of females of *C. (S.) hieroglyphicus* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would generate if it varied independently. For explanation of character codes, see text.



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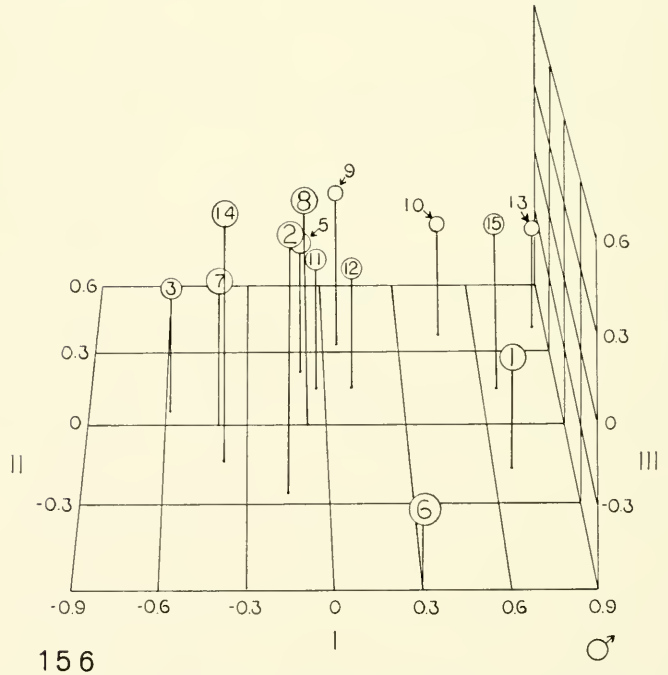


156

FIGS. **155-156.** First three principal components of 14 samples (13 in females) of *C. (S.) hieroglyphicus.*

loadings in factors IV to VIII were as follows: IV, number of tibial spines on the hind leg; V, number of antennal sensory pits; VI, length of spine d_3 in the pupa; VII, color of the respiratory horn; and VIII, number of semi-spiniform *lpm* tubercles on the penultimate abdominal segment of the pupa.

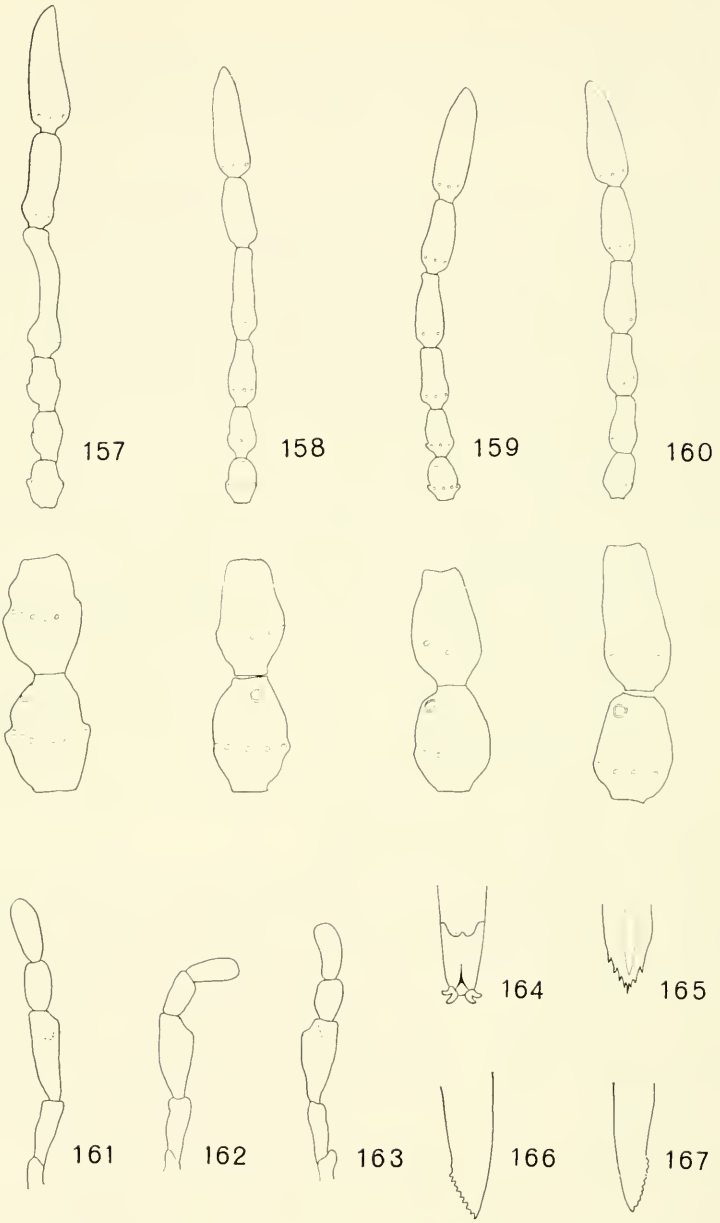
In females, nine factors were extracted which explained 76.36% of the variance. The first three, plotted in Figure 155, accounted for 58.17%. Factor I was a "general body size" component and II an *"lpm"* factor, as in the males, but III was a "dorsal spine" factor, with the lengths of spines d_1 and d_2 receiving the highest loadings. The remaining components were as follows: IV, number of multiple antennal sensory pits; V, color of the respiratory horn; VI, extent of opercular spinosity; VII, shape of the *lpm* tubercles; VIII, number of tibial spines on the hind leg; and IX, width of the respiratory horn tip.

When plots of the first three discriminant functions are compared to those of the first three principal components, a discrepancy becomes evident. The Kern County, California, population, which clusters with the southern Utah samples by discriminant functions, is quite distinct when the adults and pupae are considered together. Examination of the pupae of California forms shows they have a more spinose operculum, more spiniform *lpm* tubercles on the eighth segment and more abdominal segments with spiniform *lpm*'s than the Utah samples. Other than this, rather close agreement is noted between discriminant function analysis of the adults and the principal components study of adults and pupae together.

A critical analysis of the geographic variation patterns in pupae of *hieroglyphicus* is found in Atchley (1970).

In an earlier work (Atchley, 1967), I discussed the high incidence of *hieroglyphicus* males from Glenwood, New Mexico, possessing female characteristics, e.g., the shape of the antennae, maxillary palps, presence of mandibular teeth, etc. At the time I was unable to ascertain whether this was due to nematode parasitism, which has long been known to alter secondary sexual characteristics in male ceratopogonids, or if this was a case of evolution of host-finding organs in the males for locating females on a host, e.g., in the ears of rabbits, as in *C. utahensis*. Subsequent collecting at Glenwood has shown the great majority of males exhibiting this peculiar form of phenotypic variation were parasitized by mermithid nematodes.

As noted in the morphology section, a transition in flagellomere shape occurs between antennomeres 12 and 13 in males and 10 and 11 in females. The proximal 10 flagellomeres in males are encircled by a shelf at about their midpoint and a whorl of verticils. The shelf is lacking in females and the number of verticils is greatly reduced. The males have sensory pits on antennomeres 3, 8 and 10, the females on 3 and 5-10.



FIGS. **157-167.** Mermithid parasitized males of *Culicoides (Selfia) hieroglyphicus*. **157,** distal five flagellomeres and enlarged drawings of antennomeres 10 and 11 of normal male; **158-159,** male flagellomeres showing varaition toward female condition; **160,** male with typical female flagellum; **161,** normal male palpus; **162-163,** male palpi showing variation toward female condition; **164-167,** labrum, epipharynx and mandibles, respectively, showing variation toward female condition.

In parasitized males, all varieties of "maleness" and "femaleness" can be found. Figures 157-160 illustrate the transition from normal male type antenna in Figure 157 through transition stages in 158 and 159 to 160, the typical female structure. Further, Figure 157 has a sensory pit formula of 3, 8 and 10, Figure 158 of 3, 6-10 and Figures 159 and 160 of 3, 5-10. Other structures exhibiting sexual dimorphism, including the bifid pretarsal claws in males, the shape of the wing, the maxillary palp and the degree of development of the mouthparts, show the same transition. The change in shape of the maxillary palp can be seen in Figures 161 to 163. With regard to the mouthparts, some males have the labrum bearing median teeth but no lateral ones (Fig. 164) and have denticulate mandibles and hypopharynx (Figs. 165-167).

This phenomenon is apparently restricted to males, since in *hieroglyphicus,* as well as other *Culicoides* in which mermithid parasitism has been reported, no alteration in the secondary sexual characters in females has been noted. The male genitalia have never been found to be altered by parasitism. In *Chironomus,* however, intersexes have been reported based on both sexes (Rempel, 1940; Wülker, 1961). The degree to which the male phenotype is altered apparently depends on the stage in the life cycle in which the fly becomes infected and how far development has proceeded in any given organ.

Culicoides (Selfia) jacksoni Complex

The *jacksoni* group includes *jacksoni* n. sp., *tenuistylus* and *jamesi.* The first two species are more similar to each other than to *jamesi;* however, several structures indicate that *jamesi* should be included in this group.

The basimere of the three species is elongate and lacks a dense patch of setae on the mesal face. The basimeric roots are distinctive in that there is a hook-like process on the posterior margin. In *jamesi* a rugose membrane arises from the posterior margin of the root and attaches to the aedeagus; in *tenuistylus* a globular projection lies in the crotch of the process. In *jacksoni* there are no such modifications. The anterior end of the basimere is shelf-like in *tenuistylus,* but in the other two species only the mesal corner is sclerotized. The apices of the telomeres are simple in *tenuistylus,* slightly expanded in *jacksoni,* and greatly enlarged into a foot-shaped structure in *jamesi.*

The aedeagus is elongate in this group. In *jacksoni* and *tenuistylus* it is eversible and has a horizontal piece conecting the aedeagal arms at about midlength, which bears a posterior connection for the ejaculatory duct. The ninth sternum is unmodified in *tenuistylus* but emarginate or cleft in the remaining two species. The claspettes of *jacksoni* and *jamesi* are greatly extended posteriorly, while in *tenuistylus* this is not the case.

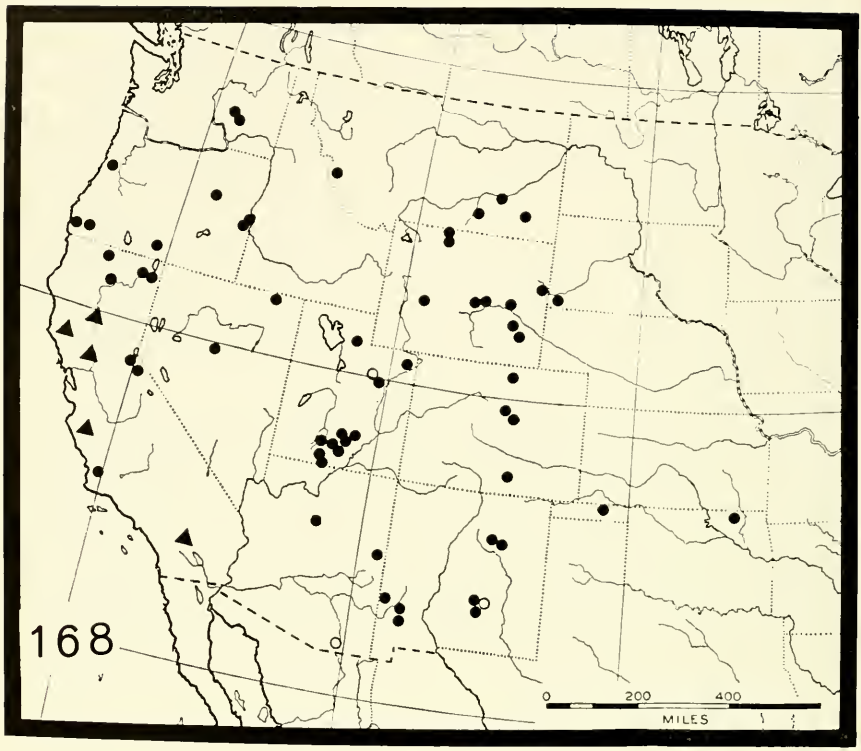


FIG. 168. Known distribution of the *Culicoides (S.) jacksoni* complex. Open circles=*C. (S.) jacksoni;* closed circles=*C. (S.) jamesi;* triangles=*C. (S.) tenuistylus.*

The abdominal tubercles of the pupae generally have their bases rounded in this group, although occasionally they may be semi-spined. There is a mesal lobe between the genital sheaths on the anal segment of the males.

In the larvae the frontal comb of the epipharynx has numerous sharp teeth.

Culicoides tenuistylus and *C. jacksoni* have rather restricted distributions, the former found only in California, the latter known only from two localities in the higher elevations of Utah and New Mexico and a third in southern Arizona (Fig. 168).

Culicoides jamesi is widely distributed over most of the western United States.

Culicoides (Selfia) jacksoni new species
(Figs. 169-198)

This description is based on 19 females and 15 males from Ruidoso, New Mexico (type locality), all except three males reared from larvae or pupae.

FEMALE—Length of wing 1.16 mm (1.08-1.20, ±0.036; n=14); width 0.56 mm (0.53-0.59, ±0.023; n=14).

Head: Vertex with numerous long setae. Eyes rather narrowly separated, width of separation rarely greater than 0.25 of length (Fig. 180). Antennal flagellomeres in proportion of 12:10:10:10:10:10:10:10:13:13:14:14:23; proximal eight flagellomeres roughly 1.25 times as long as wide (Fig. 181); total length of flagellum 480μ (430-500, ±21.0; n=14); antennal ratio 0.93 (0.87-1.0; n=14); antenonmeres 9+10 to 11 in ratio of 0.62 (0.55-0.65; n=14); distal sensory pits present on antennomeres 3-10, occasionally absent from 4; multiple sensory pits rarely present on antennomeres other than 3. Distal four palpal segments in proportion of 16:22:10:12; third segment moderately swollen, 2.2 (1.8-2.4; n=14) times as long as greatest breadth, with a deep sensory pit (Fig. 178). Total length of head 340μ (300-370, ±17.0; n=14); ratio of head length to proboscis 1.24 (1.18-1.33; n=14). Mandibles with 12 (11-13; n=14) teeth. Maxillae with 14 (13-16; n=14) teeth.

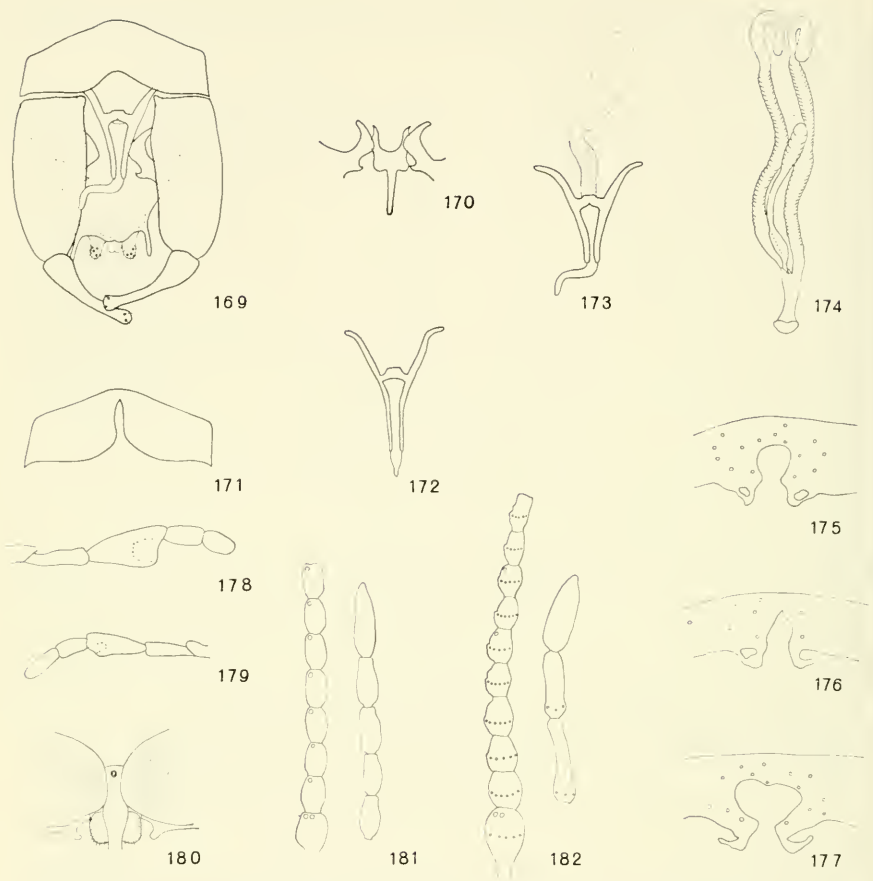
Thorax: Legs light brown, femorotibial slightly darker; no distinct banding. Hind leg with segments in proportion of 55:25:134:131:69:31:19:12:16; hind tibial comb with four spines; basal four tarsomeres on hind leg with distal spine. Stigma of wing brownish. Macrotrichia strong, numerous over majority of cells and veins, most abundant at anterior margin of cell R_5. Costa extending 0.54 (0.53-0.57; n=14) of entire wing length.

Abdomen: Light brown. Eighth sternum with large, deep posterior median pocket bordered postero-laterally by laterally directed processes (Fig. 177), latter sometimes fused to caudal margin of eighth sternum producing two minute elliptical unsclerotized areas (Figs. 175-177). Spermathecae three (Fig. 174); two very long, finger-like, faintly sclerotized, extending anteriorly into sixth abdominal segment, measuring 305 and 294μ respectively from the common duct; third spermatheca shorter, more slender, distally swollen, measuring 140μ from union with common duct.

MALE—Length of wing 0.99 mm (0.96-1.02, ±0.024; n=7); width 0.41 mm (0.37-0.42, ±0.017; n=7).

Head: Brown. Antenna with flagellomeres in proportion of 17:11:11:10:10:10:10:10:10:12:26:20:24 (Fig. 182); distal sensory pits on antennomeres 3, 8 and 10, occasionally on 4, 5 and/or 6; flagellar length 560μ (540-590, ±23.0; n=6). Distal four palpal segments in proportion of 12:17:9:12 (Fig. 179); third segment slightly swollen, 2.52 (2.29-2.83; n=7) times as long as greatest breadth, with a small, deep sensory organ. Head length 320μ (290-350, ±23.0; n=6).

Thorax: Legs light brownish, lacking distinct banding pattern. Segments of hind legs in proportion of 53:23:120:119:62:29:18:12:15. Hind tibial comb with four, occasionally five, spines; basal four tarsomeres on hind



FIGS. **169-182.** *Culicoides (Selfia) jacksoni* n. sp. **169,** male genitalia, claspettes removed; **170,** claspettes; **171,** "cleft" ninth sternum of male; **172,** aedeagus in uneverted condition; **173,** aedeagus in everted condition with ejaculatory duct and accessory gland; **174,** spermathecae; **175-177,** variation in female eighth sternum; **178,** female palpus; **179,** male palpus; **180,** female eye separation; **181,** female flagellum; **182,** male flagellum.

leg with distal spine. Stigma of wing light gray. Macrotrichia short, rather abundant in cell R_5, less numerous in M_1 and few in M_2; macrotrichia absent in cell M_4, vannal cell, on vein M_{3+4}+Cu_1 based to medio-cubital fork and Cu_1 and Cu_2. Costa extending 0.48 (0.46-0.51; n=7) of entire wing length.

Genitalia (Figs. 169-173): Ninth tergum strongly tapering posteriorly, caudal margin convex with slight mesal cleft; two large preapical setigerous lobes lying between cleft and very slender, elongate, slightly divergent apico-lateral processes. Ninth sternum with caudo-mesal emargination varying from rather broadly open (holotype, Fig. 169) to deep, narrow cleft (Fig.

171). Basimere oblong, about 2.5 times as long as broad, with numerous long setae on ventral face; basimeric root large, foot-shaped, "heel" portion stout, "toe" more slender, projecting antero-laterally; posterior edge of root with distinct mesally directed hook-like process; postero-medial surface of root articulating with anterior arms of claspettes; anteromesal corner of basimere heavily sclerotized, articulating with arms of aedeagus. Telomere with swollen, setose base; median portion narrowed and slightly swollen. Aedeagus elongate, A-shaped; median posterior process tapering caudally, more or less pointed distally, in uneverted condition (Fig. 172); anterior arms slender, strongly divergent, basal ends turned laterad; top of aedeagal arch concave, formed by horizontal cross-bar between aedeagal arms; median opening present connecting aedeagus to ejaculatory duct. Claspettes fused; median posterior process greatly extended, almost as long as remainder of structure, bounded basally by prominent shoulders; anterior process elongate, slender, slightly sinuate, tapering anteriorly.

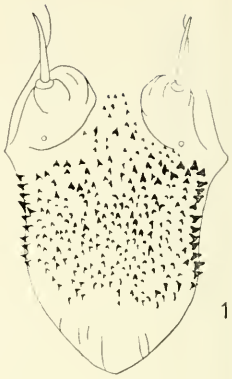
PUPA: Light brown to brownish. Quantitative characters summarized in Table 15.

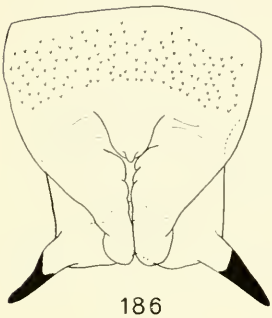
Respiratory horn (Fig. 183): Arising from distinct pedicel with single straight trachea. Apex very dark and somewhat expanded; median one-third light brown to dark yellow, basal one-third darker; sometimes basal two-thirds of horn more or less uniformly brown. Lateral spiracular openings often slightly darker; two, occasionally three, well separated lateral spiracular openings. Lateral convolutions distinct only in median one-third of horn; scales most distinct above convolutions.

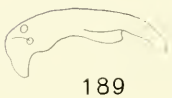
Operculum (Fig. 184): Brown; opercular teeth darker, generally covering majority of opercular face; larger, heavier teeth (Fig. 185) confined to lateral margins and areas immediately above *am* tubercles; teeth of inner area of face smaller; spines occurring between and sometimes slightly beyond *am* tubercles; *am* tubercle well developed.

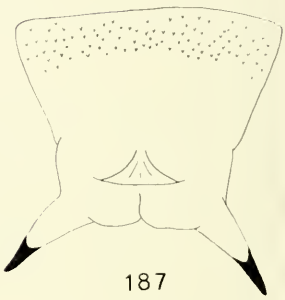
Cephalic-thoracic chaetotaxy: Basal portion of antennal sheath and *ad* tubercle region brown, apical portion of antennal pad lighter brown; ventral region of head pale brown to pale yellow. Tubercles of thorax rounded except bases of d_1 and *ad* spiniform. *Dorsals* with well developed spines (Fig. 195), tip of spine d_1 usually overlapping tubercle d_2; d_3 with long, well developed spine. Tubercle *dl* with two spines (Fig. 193), one long, filamentous, second shorter, stouter. Tubercle *ad* (Fig. 196) with two spines, one long, very stout, other shorter, thinner. Two *vm* spines, posterior spine approximately twice as long and stout as anterior spine. Two long filamentous, subequal *vl* spines (Fig. 190).

Abdomen: Tubercles generally with rounded or truncated apices; apices of *lpm* tubercles of eighth and *lasm* of seventh segments occasionally semi-spined, latter rarely spiniform (Figs. 191, 198), *dpm* tubercles 3 and 4 lacking









FIGS. 183-189. *Culicoides (Selfia) jacksoni* n. sp. **183,** pupal respiratory horn; **184,** female operculum; **185,** silhouette of opercular teeth; **186,** last abdominal segment of male pupa; **187,** last abdominal segment of female; **188,** larval epipharynx; **189,** larval mandible.

spines (Fig. 194); *vpm's* as in Figure 192; *dasm's* as in Figure 197. Anal segment of both sexes with anterior circumsegmental band of spicules (Figs. 186-187), postero-lateral processes widely divergent, posterior margin of segment with prominent medial cleft; genital sheaths of male prominent, distally rounded, apices turned outward parallel to axis of body; a pronounced lobe between bases of genital sheaths with a small, distinctive median posterior protuberance.

LARVA:

Mandible (Fig. 189): Base broad, apex curved, pointed; a shelf-like process on inner surface of tooth; two rather large, spherical clear areas on base, a fine seta arising from one. Mandible 46μ (45-48, $\pm$1.3; n=5) long.

Epipharynx (Fig. 188): Well sclerotized. Lateral arms with proximal ends arising almost parallel to each other, then turned laterally and anteriorly to produce prominent "shoulders" before projecting postero-laterally; apex turned laterad, terminating with rather bulbous tip; distance between

tips of lateral arms 65μ; a fringe of minute hairs arising from anterior margin of shoulders of lateral arms; sclerites forming dorsal combs apparently contiguous; dorsal comb with 6-7 strong teeth; width of combs at widest point 20μ; frontal comb with 7 teeth; median teeth stronger than lateral ones.

DISTRIBUTION: This species to date has been collected in two high mountain localities in northeastern Utah and southern New Mexico and taken at light in the Huachuca Mountains of Arizona.

Specimens examined:

Holotype male with associated pupal skin, NEW MEXICO, Lincoln County, Ruidoso, Cedar Creek Canyon, 7100 ft., 13 July 1968, W. R. Atchley, S-1106, reared; allotype female with associated larval and pupal skins, W. R. Atchley, S-1148, same data as holotype. Holotype, allotype and paratypic series deposited in USNM. Remaining paratypes in Snow Museum of the University of Kansas. Paratopotypes, 9 males, 19 females, each with associated pupal skin, 4 of females also with associated larval skin; 3 males, same locality, 6 June 1965, light, W. R. Atchley. UTAH: Duchesne County, Willow Creek, 12.5 mi. N. Castle Gate, 7600 ft., 12 July 1968, W. R. Atchley, reared, 5 males, 6 females, each with associated pupal skin. ARIZONA: Cochise County, Ramsey Canyon, Huachuca Mts., July 1967, W. Brown, light, 2 males.

On rare occasions in one's academic career he is influenced by a professor who, by his enthusiasm and interest in his students, is able to open new and challenging vistas to them. Dr. R. C. Jackson, Professor of Botany, University of Kansas, for whom this species is named, has been able to instill in his students the idea that systematics need not necessarily be a sterile exercise confined to studying species and populations as static assemblages. Instead, by emphasizing an experimental approach utilizing such tools as cytogenetics and hybridization, he has stressed that species exist in nature as groups of constantly evolving gene pools which can be crossed and meaningful questions answered about their genetic relationships.

Culicoides (Selfia) tenuistylus Wirth

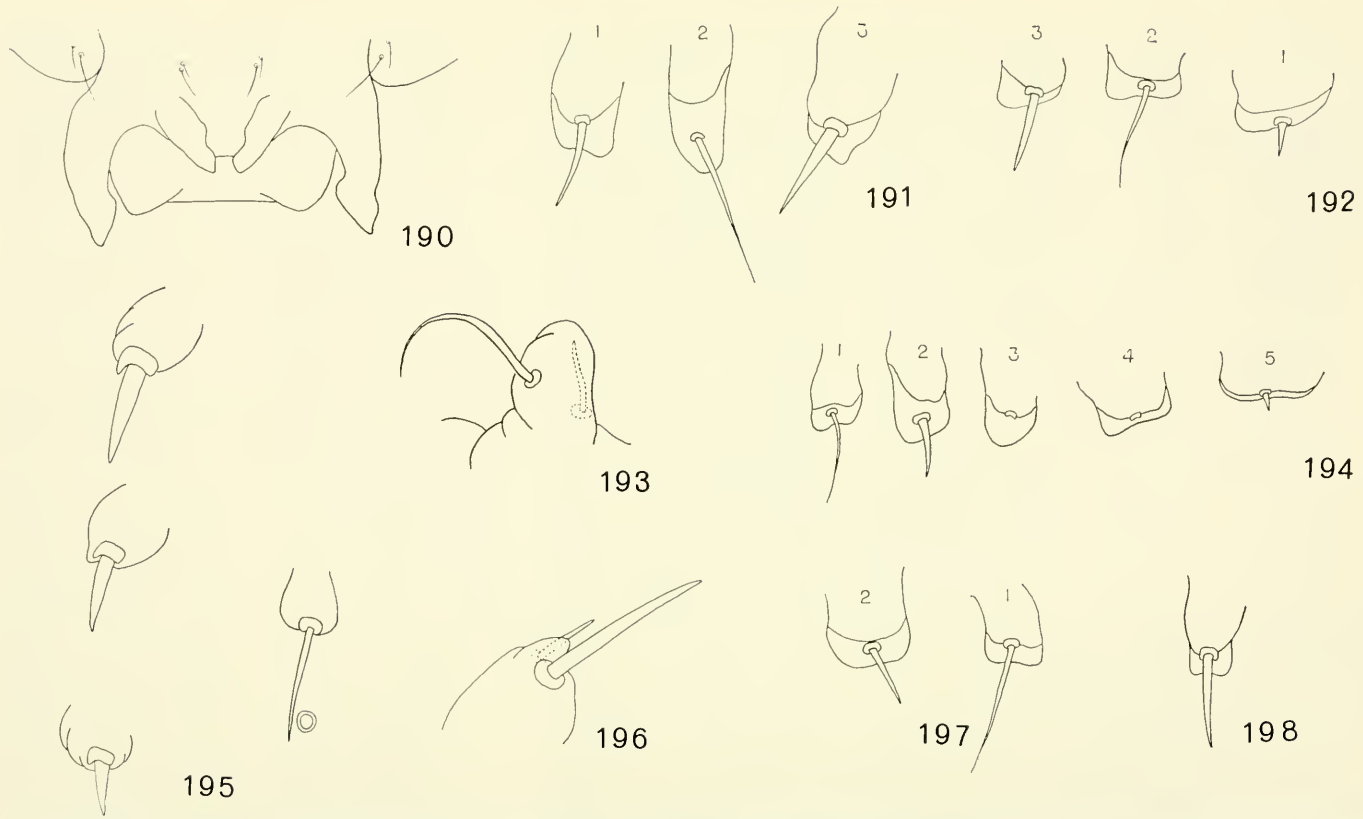
(Figs. 3, 11, 199-215)

Culicoides tenuistylus Wirth, 1952, Univ. Calif. Pub. Ent. 9:175-179 (male, female; Wheeler's Springs, Ventura Co., California; fig. palpus, male genitalia).
Culicoides (Selfia) tenuistylus; Khalaf, 1954, 38.

The following description of adults is based on the original type series as well as other materials available from California. The immature stages are described from specimens collected at Hopland, California.

FEMALE—Length of wing 1.26 mm (1.11-1.49, $\pm$0.103; n=20); width 0.58 mm (0.54-0.64, $\pm$0.039; n=6).

Head: Vertex with several long setae. Eye separation rather broad, width of separation about 0.40 of length (Fig. 203). Antennal flagellomeres in proportion of 14:10:10:10:10:10:10:10:15:15:16:17:25; proximal eight flagellomeres about 1.25 times as long as broad (Fig. 207); total length of flagellum 501μ (443-617, $\pm$49.3; n=19); antennal ratio 1.0 (0.91-1.10; n=14); flagellomeres 9+10 to 11 in ratio of 0.67 (0.63-0.74; n=15); distal



FIGS. **190-198.** *Culicoides (Selfia) jacksoni* n. sp. **190,** *vm* and *vl* setae; **191,** *lpm* tubercles; **192,** *vpm* tubercles; **193,** *dl* tubercle; **194,** *dpm* tubercles; **195,** *d* tubercles; **196,** *ad* tubercles; **197,** *dasm* tubercles; **198,** *lasm* tubercle.

sensory pits on antennomeres 3-10, occasionally absent from 4; multiple sensory pits on 7-10, sometimes on 6 also (but see section on variation). Distal four palpal segments in proportion of 16:24:10:11; third segment moderately swollen, 2.2 (2.0-2.5; n=13) times as long as greatest breadth, with a deep sensory organ (Fig. 206). Total length of head 353μ (304-391, $\pm$22.9; n=21); ratio of head length to proboscis 1.27 (1.1-1.4; n=15). Mandibles with 12 (11-13) teeth. Maxillae with 16 (15-17) teeth.

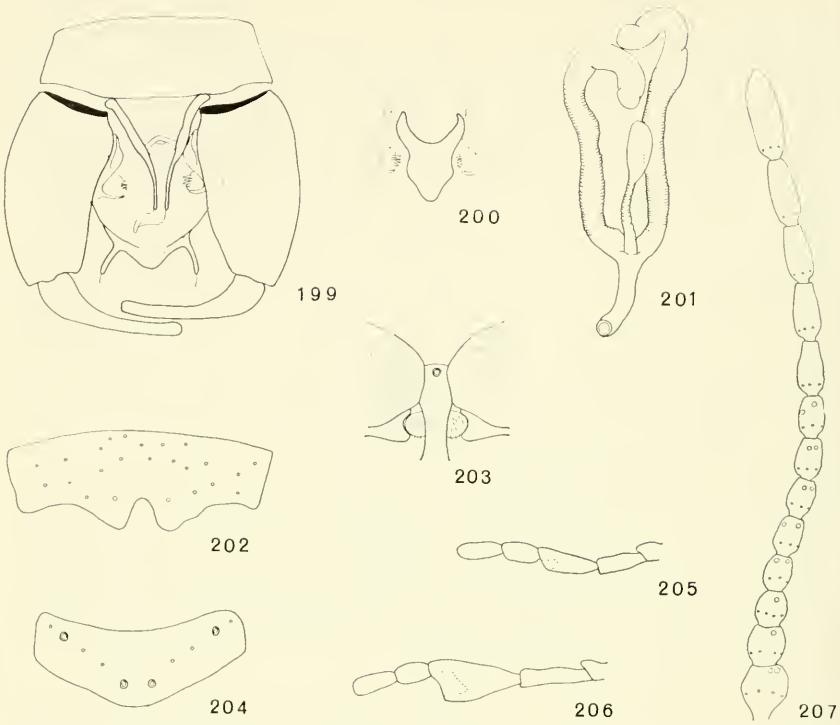
Thorax: Mesonotum dark brown with pale grayish markings; a dark brown median stripe, bounded laterally by a pair of longitudinal, submedian paler bands extending approximately two-thirds of length of disc; dark bands projecting laterally and posteriorly from the humeral pits; smaller, grayish areas on either side of lateral humeral dark band. Legs brown to dark brown, tarsi often slightly paler; often a rather faint subbasal pale band on fore tibia; femorotibial joint dark. Hind leg with segments in proportion of 60:25:143:140:74:34:20:13:16; hind tibial comb with four or rarely five spines, no one spine distinctly longer than any other; basal four hind tarsomeres bearing distal spine. Scutellum with one pair median, one pair lateral macrosetae; two pairs (rarely one) interior, one pair exterior microsetae (Fig. 204). Stigma of wings brownish. Macritrichia abundant over majority of veins and cells. Costa extending 0.58 (0.55-0.62; n=14) of entire wing length.

Abdomen: Brown. Eighth sternum with shallow postero-median pocket; postero-lateral margins of pocket simple (Fig. 202). Ninth sternum with anteromesal thumb-like projection. Spermathecae three (Fig. 201); two long, subequal, tubular, measuring 232 and 245μ respectively, median portion with annulated pattern which is absent on apical third; third spermatheca shorter, anteriorly bulbous, 108μ long; bursa 62μ in length, with single broad posterior opening.

MALE—Length of wing 1.09 mm (1.01-1.24, $\pm$0.026; n=6); width 0.43 mm (0.37-0.48, $\pm$0.045; n=4).

Head: Brown. Antennal flagellomeres in proportion of 16:12:12:10:10: 10:10:10:10:10:30:20:26; distal sensory pits on antennomeres 3, 7-10, multiple sensory pits rarely occurring on other than 3; length of flagellum 599μ (558-651, $\pm$31.8; n=6). Distal four palpal segments in proportion of 12:15:9:12 (Fig. 205), third segment with small, deep sensory organ. Head length 327μ (310-356, $\pm$17.7; n=6).

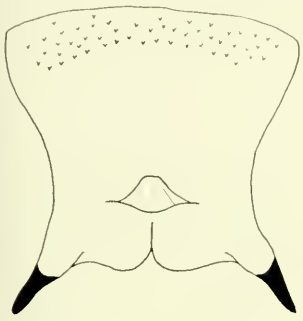
Thorax: Legs brown, femorotibial joint dark. Hind leg with segments in proportion of 50:23:130:131:67:32:18:12:15; hind tibial comb with four spines; basal four hind tarsomeres with distal spine. Scutellum with one pair median, one pair lateral macrosetae; one pair interior microsetae present. Stigma of wing pale brown. Macrotrichia apparently absent from cell

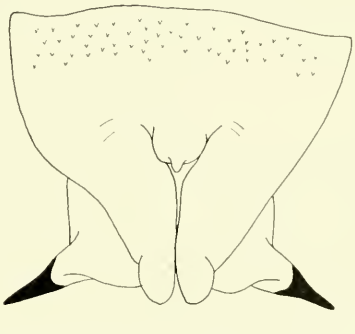


FIGS. **199-207.** *Culicoides (Selfia) tenuistylus* Wirth. **199,** male genitalia, claspettes removed; **200,** claspettes; **201,** spermathecae; **202,** eighth sternum of female; **203,** female eye separation; **204,** female scutellum; **205,** male palpus; **206,** female palpus; **207,** female flagellum.

M_4 and vannal cell but present on veins M_{3+4} and Cu_1. Costa extending 0.50 (0.48-0.54; n=6) of entire wing length.

Genitalia (Figs. 199-200): Ninth tergum markedly tapered posteriorly; caudal margin quite convex and no evidence of medial notch; apicolateral processes slender, elongate, divergent; tergum clothed with numerous long setae. Ninth sternum simple, lacking caudal emargination or posteriorly projecting processes. Basimere oblong, covered with numerous long setae; basal portion not distinctly swollen; basimeric root distally enlarged and foot-shaped, with lateral rib; a long, slender, slightly curved process arising from postero-median edge, with a ball-shaped structure bearing several finger-like projections in cephalic depression. Telomere expanded basally, bent mesally with simple apex lacking spine or other modification; about 0.75 as long as basimere. Aedeagus elongate, A-shaped, eversible; lateral arms more or less straight, diverging anteriorly; horizontal piece connecting arms anteriorly convex and bearing a median opening; membrane bare. Claspettes fused (Fig. 200), triangular; lateral margins sinuate, apex blunted; anterior arch broad and rather deep.





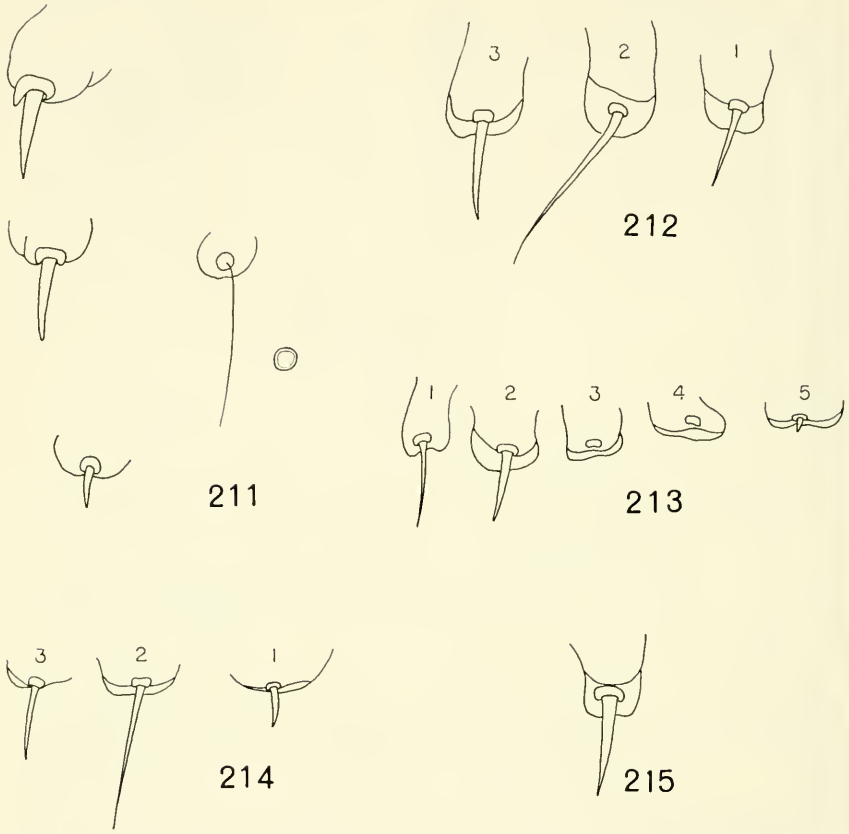
Figs. **208-210.** *Culicoides (Selfia) tenuistylus* Wirth. **208,** pupal respiratory horn; **209,** last abdominal segment of female pupa; **210,** last abdominal segment of male.

PUPA: Brownish. Quantitative characters summarized in Table 16.

Respiratory horn (Fig. 208): Arising from prominent pedicel and containing a single trachea. Apex dark, approximately same width as remainder of horn. Two lateral spiracles opening on well-separated protuberances, outer protuberance more pronounced than inner one; lateral protuberances slightly darker than remainder of horn. Lateral convolutions distinct only distal to last lateral spiracular opening.

Operculum: Brown; strongly denticulate, teeth extending between and beyond *am* tubercles; stronger teeth confined to lateral margins. Tubercles and spines well developed.

Cephalic-thoracic chaetotaxy: Tubercle *ad* and antennal pad dark, latter lighter apically. Tubercles *ad* and d_1 with bases spiniform, other tubercles rounded. Distance between sockets of d_1 and d_2 less than distance between d_2 and d_3 (Fig. 211). Two pairs of *vl* and *vm* spines.



FIGS. 211-215. *Culicoides (Selfia) tenuistylus* Wirth. **211,** *d* tubercles; **212,** *lpm* tubercles; **213,** *dpm* tubercles; **214,** *vpm* tubercles; **215,** *lasm* tubercle.

Abdomen: All abdominal tubercles with bases rounded (Figs. 212-215); *dpm* tubercles 3 and 4 lacking spines. Anal segment of both sexes with short lateral processes (Figs. 209-210); genital lobes of males simple distally, possessing only slight apical bend; mesal lobe at base of sheath with median posterior protuberance.

LARVA: Head length 174μ (n=2); width 108μ (n=2); width of oral ring 84μ (n=1); head ratio 1.60 (n=2); length of mandible 44μ (n=2). For chaetotaxy see Figure 11 and Morphology section.

DISTRIBUTION: Present records indicate this species is restricted to California.

Specimens examined:

Holotype male, allotype female and 6 paratypes from USNM collections, Wheeler's Springs, Ventura County, California, 16 June 1948, W. W. Wirth, light; 1 male, 1 female paratype, Piru Canyon, Ventura County, 22 April 1948, R. Coleman, light; same locality, 25 April 1948, R. Coleman, light, 7 males, 6 females. Monterey County, Kings City, 26-28 June 1948, W. W.

Wirth, light, 1 male, 1 female (male is paratype); Mendocino County, Hopland, 19-22 May 1964, reared from sandy stream margin, 3 males, 12 pupae, 2 larvae; Hopland, 14 May 1964, 18 females (10 *ex* ear of deer, 2 *ex* ear of jackrabbit). Tehama County, Red Bluff, 23 April 1949, light, 1 male, 6 females. Yolo County, Davis, 16-22 May 1950, 2 males.

VARIATION: From the limited amount of material available, it is evident that two morphs exist, one more common in the northern part of California, the other more prevalent in the southern part. The most evident distinguishing features are size, as indicated by wing length, length of flagellum and length of head, and the number of multiple sensory pits on the antennae. The former is responsible for the abnormally large standard deviation of the wing and flagellar lengths. The larger northern forms possess a total of eight to twelve multiple pits on both antennae, while the smaller southern forms have up to two multiple sensory pits. There are two exceptions to this, one from Kings City and the other from Red Bluff, that more resemble their counterparts than they do the individuals from their own locality. The lack of reared associated material of this species prevents a critical analysis of this problem and, therefore, these two forms can only be referred to as "morphs" for the time being.

Culicoides (Selfia) jamesi Fox
(Figs. 216-240)

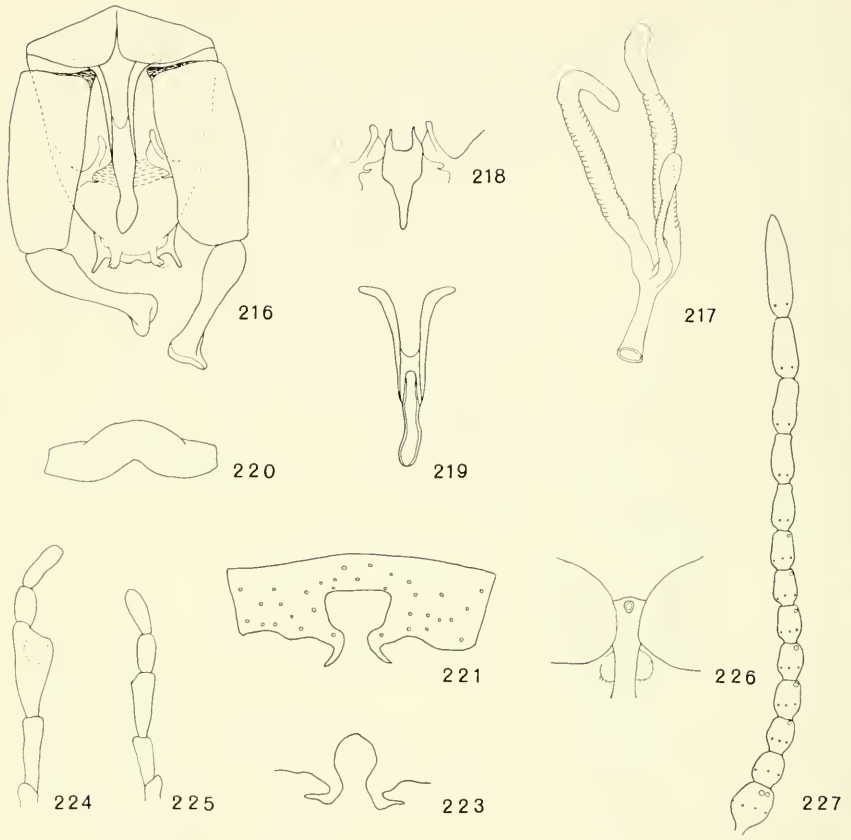
Culicoides jamesi Fox, 1946, Proc. Ent. Soc. Wash. 48:244 (male, female; Hamilton, Montana; figs. mesonotum, wing, palpus, male genitalia).
Culicoides (Selfia) jamesi; Khalaf, 1954, 38.

The following description is based on 45 specimens reared from larvae or pupae from three localities in eastern Wyoming: northwest of Wheatland, Platte County; Boxelder Creek, southeast of Glenrock, Converse County; and Stockade Beaver Creek, east of Newcastle, Weston County.

FEMALE—Length of wing 1.21 mm (1.14-1.39, ±0.08; n=25); width 0.58 mm (0.55-0.65, ±0.04; n=25).

Head: Vertex with several long setae. Eye separation moderately broad (Fig. 226), width of separation about 0.30 of length. Antennal flagellomeres in proportion of 13:9:9:9:9:9:9:13:13:14:16:27; proximal eight flagellomeres approximately 1.25 times as long as broad (Fig. 227); total length of flagellum 510μ (480-536, ±24.5; n=18); antennal ratio 1.0 (0.90-1.08; n=25); flagellomeres 9+10 to 11 in ratio of 0.63 (0.59-0.70; n=25); distal sensory pits present on antennomeres 3-10, occasionally absent from 4; one or two multiple sensory pits rarely present. Distal four palpal segments in proportion of 16:26:11:14; third segment moderately swollen, 2.46 (2.1-2.8; n=18) times as long as broad, with a deep sensory organ (Fig. 224). Total length of head 368μ (350-388, ±10.4; n=18); ratio of head length to proboscis 1.14 (1.09-1.27; n=18). Mandibles with 12 (11-13) teeth. Maxillae with 16 (15-17) teeth.

Thorax: Legs brownish, often with a faint pale subbasal band on fore



FIGS. 216-227. *Culicoides (Selfia) jamesi* FOX. **26,** male genitalia, claspettes removed; **217,** spermathecae; **218,** claspettes; **219,** aedeagus; **220,** ninth sternum of male; **221, 223,** eighth sternum of female; **224,** female palpus; **225,** male palpus; **226,** female eye separation; **227,** female flagellum.

tibiae; femorotibial joint dark. Hind leg with segments in proportion of 60:25:138:136:73:34:20:12:16; hind tibial comb with four or occasionally five spines; basal four hind tarsomeres with distal spine. Scutellum with one pair median and one pair lateral macrosetae; 2-4 pairs microsetae, one pair always exterior, others usually interior. Stigma of wing light brownish. Macrotrichia abundant on majority of veins and cells. Costa extending 0.56 (0.54-0.58; n=25) of entire wing length.

Abdomen: Eighth sternum with rather deep postero-median pocket (depth often difficult to discern); postero-lateral corners of pocket projected into laterally directed hook-like processes (Figs. 221, 223) (some California and New Mexico specimens lack processes). Ninth sternum with antero-mesally directed thumb-like projections. Spermathecae three (Fig. 217);

outer two elongate, tubular, 228 and 240μ in length with median half more or less annulate; third spermatheca shorter, anteriorly expanded, 124μ long; bursa 72μ long, with large posterior opening.

MALE—Length of wing 1.09 mm (0.95-1.21, ±0.086; n=16); width 0.44 mm (0.39-0.48, ±0.028; n=16).

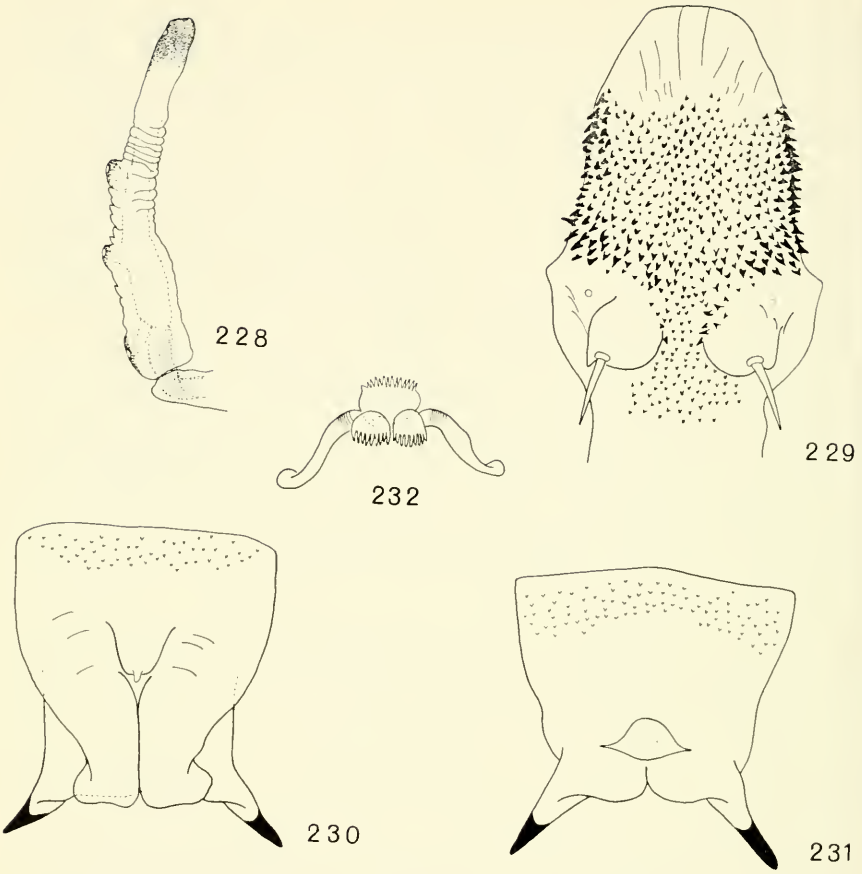
Head: Antennal flagellomeres in proportion of 19:12:11:11:10:10:10:10:10:11:28:22:25; distal sensory pits on antennomeres 3, 6, 8 and 10, occasionally absent from 6 or present on 5; multiple sensory pits absent; flagellar length 602μ (518-682, ±44.5; n=13). Distal four palpal segments in proportion of 12:19:10:13; third segment with small, deep sensory organ (Fig. 225). Head length 332μ (301-356, ±15.5; n=13).

Thorax: Legs brownish, often with a faint subbasal pale band on fore tibiae; femorotibial joint dark. Hind leg with segments in proportion of 52:23:129:67:32:20:15; hind tibial comb with four spines; hind tarsomeres with distal spines. Scutellum with one pair median and one pair lateral macrosetae and one pair of interior microsetae. Stigma of wing very faint brown. Macrotrichia absent from cell M_4 and vannal cell but present on veins M_{3+4} and Cu_1. Costa extending 0.49 (0.42-0.52; n=16) of entire wing length.

Genitalia (Figs. 216, 218-220): Ninth tergum narrowing posteriorly; caudal margin convex, with slight mesal notch; apicolateral processes slender, elongate, slightly tapering, strongly divergent. Ninth sternum short at lateral margins, long mesally, median portion with very deep cleft, almost completely dividing sternum, or with rather shallow posterior emargination (Fig. 220). (Both forms of the sternum occur in most populations and at present little sense can be made of the variation.) Basimere elongate, long setae present on mesal face but not as dense as in some other species; basimeric root arcuate, posterior margin strongly convex with a shelf along lateral one-third; small hook-like projection arising mesally on posterior surface of root; rugose membrane connecting roots and aedeagus. Telomere with prominent, laterally turned, foot-shaped apex. Aedeagus markedly elongate with faint subapical constriction making apex appear slightly bulbous; median posterior process trough-like and noneversible, apical and invaginated, producing short duct apparently connected to ejaculatory duct (Fig. 219). Claspettes fused (Fig. 218); median portion elongate, diminishing caudally; fused body stout with short, tapering anterior process.

PUPA: Light brown. Quantitative characters summarized in Table 17.

Respiratory horn (Fig. 228): Arising from distinct pedicel and containing a single trachea. Apex dark, usually about same width as remainder of horn. Three lateral spiracular openings, outer two on distinct, unarmed protuberances; basal protuberance not prominent. Later convolutions generally most evident distal to last lateral spiracular opening.



FIGS. **228-232.** *Culicoides (Selfia) jamesi* Fox. **228,** pupal respiratory horn; **229,** female operculum; **230,** last abdominal segment of male pupa; **231,** last abdominal segment of female; **232,** larval epipharynx.

Operculum (Fig. 229): Densely denticulate, teeth abundant between and posterior to *am* tubercles and often on tubercles; strong teeth generally confined to lateral margins.

Cephalic-thoracic chaetotaxy: All tubercles except *ad*, d_1 and occasionally d_2 with rounded bases. Distance between sockets of d_1 and d_2 less than that between d_2 and d_3 (Fig. 238). Two pairs of *vl* and of *vm* spines (Fig. 233). Tubercle *dl* as in Figure 234.

Abdomen: All tubercles with rounded bases (Figs. 235-240); occasionally some of *lpm* with tubercle bases "semi-spined"; *lasm* with base occasionally "semi-spines," rarely "spined." Anal segment of both sexes with prominent, divergent, lateral processes (Figs. 230-231); genital sheaths of male with

Figs. **233-240.** *Culicoides (Selfia) jamesi* Fox. **233,** *vm* and *vl* setae; **234,** *dl* tubercle; **235,** *lpm* tubercles; **236,** *dasm* tubercles; **237,** *vpm* tubercles; **238,** *d* tubercles; **239,** *lasm* tubercle; **240,** *ad* tubercle.

distinct apical modification, apex strongly truncate with lateral expansion (Fig. 230); mesal lobe at base of sheaths, possessing a median posterior protuberance.

LARVA:

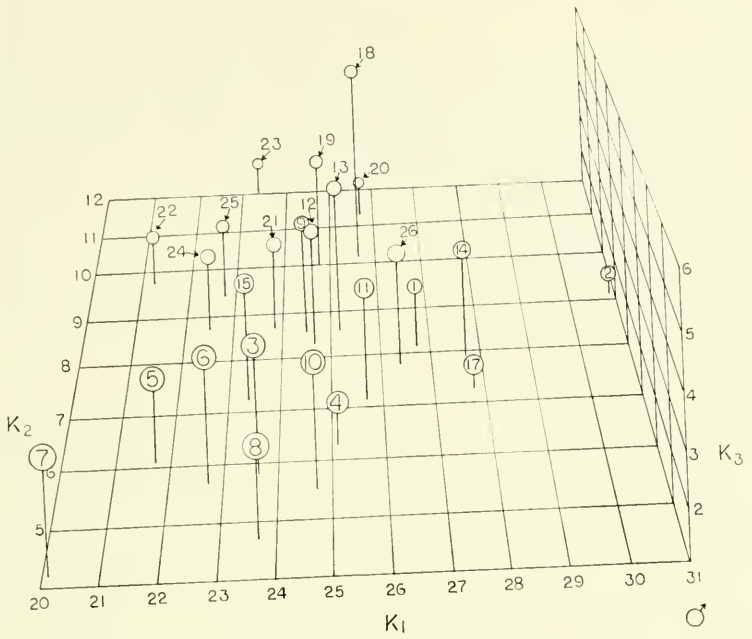
Epipharynx (Fig. 232): Lateral arms moderately stout; dorsal comb with nine stout teeth; frontal comb with 14-15 sharp, smaller teeth often alternating with stronger teeth; a small fringe of delicate hairs on shoulders of lateral arms.

TYPE: The holotype of *jamesi* is in the collections of the School of Public Health and Tropical Medicine of the University of Puerto Rico.

DISTRIBUTION: Culicoides jamesi is distributed as in Figure 168.

Specimens examined:

ARIZONA: Apache County, Springerville, 2 July 1953, 6900 ft., light, 5 males, 17 females. Cocconino County, Oak Ck. Canyon, 22 July 1959, light, 1 male. CALIFORNIA: Alpine County, Coleville, July 1948, light, 9 males. Alpine County, Topaz Lake, July 1948, light, 6 males, 5 females. Eldorado County, Snowline Camp, 13 July 1948, light, 2 females. Lassen County, Hallelujah Jct., 18 July 1953, 3 males, 1 female. Modoc County, Alturas, June 1948, light, 2 males. San Luis Obispo County, 2 mi. N. Cuyama, reared, 5 males, 5 females, each with associated pupal skin. Shasta County, Burney, 15 July 1947, 1 male. Siskiyou County, Hornbrook, Aug. 1948, light, 3 males, 5 females. COLORADO: Douglas County, Castle Rock, 27 July 1940, light, 1 male. Jefferson County, Soda Ck., reared, 4 males, 2 females, each with associated pupal skin. Huerfano County, Martin Lake, 26 July 1967, light, 1 male, 3 females. Larimer County, Ft. Collins, 26 May 1942, light, 1 male. MONTANA: Big Horn County, 12 mi. S. Custer, 2700 ft., 8 Aug. 1968, reared, 3 males, 8 females, each with associated pupal skin. Custer County, Pumpkin Ck., 30 mi. N. Volborg, 2400 ft., 8 Aug. 1968, reared, 13 males, 19 females, each with associated pupal skin. Ravalli County, Hamilton, Aug. 1940, 1 male, 1 female, PARATYPES. Rosebud County, 6 mi. W. Forsyth, 2500 ft., 8 Aug. 1968, 10 males, 6 females. NEVADA: Elko County, Hendricks Ck., S. E. Mountain City, 6200 ft., 30 July 1968, reared, 8 males, 6 females. Lander County, 5 mi. E. S. E. Austin, 6750 ft., 5 Aug. 1964, 1 male, 1 female. NEW MEXICO: Catron County, 5 mi. E. Glenwood, 24 June 1953, light, 1 male. Grants County, Roberts Lake, 31 July 1965, 2 males, 23 females. Lincoln County, Cedar Ck. Canyon, Ruidoso, 16 July 1965, 16 males, 50 females. San Miguel County, Tecolote Ck., Tecolote, 6400 ft., reared, 6 males, 3 females, Pecos, 27 June, *ex* horse, 4 females. OREGON: Benton County, Berry Ck., 14-21 July 1960, 1 male, 2 females. Clarkamas County, Aumsville, June 1963, light, 2 females. Curry County, Gold Beach, 30 June 1967, light, 1 male, 6 females. Grant County, 10 mi. S. John Day, 20 July 1967, light, 1 male, 2 females. Josephine County, Grants Pass, 13 June 1963, light, 3 females. Lake County, Lakeview, 25 Aug. 1965, light, 1 female. Malheur County, Little Valley, S. W. Vale, 19 June 1963, light, 2 females. SOUTH DAKOTA: Fall River County, Oral, 4 July 1953, 1 male. UTAH: Duchesne County, Willow Ck., 12 mi. N. Castle Gate, 7600 ft., 12 July 1968, reared, 11 male, 14 females, each with associated pupal skin. Garfield County, E. Fork Sevier River, 3 mi. W. Ruby's Inn, 7700 ft., 20 July 1968, reared, 4 males, each with associated pupal skin. Paria River, N. Henrieville, 6400 ft., 20 July 1968, 2 males, 5 females, each with associated pupal skin. Upper Valley Ck., 5 mi. W. Escalante, 6000 ft., 21 July 1968, reared, 3 males, 2 females, each with associated pupal skin. Pine Ck., 8 mi. N. Escalante, 6600 ft., 21 July 1968, 3 males, 4 females, each with associated pupal skin. Escalante River, 15 mi. E. Escalante, 5100 ft., 21 July 1968, 2 males, 5 females. Kane County, Kanab Ck., 7 mi. N. Kanab, 5200 ft., 19 July 1968, reared, 1 male with associated pupal skin. E. Fork Virgin River, Mt. Carmel Jct., 5300 ft., 23 July 1968, reared, 2 males, 2 females, each with associated pupal skin. Morgan County, 16 mi. S. Wasatch, 27 July 1968, 5700 ft., reared, 1 male, 4 females, each with associated pupal skin. Uintah County, Green River, Dinosaur Nat'l. Mont., 4500 ft., 9 July 1968, reared, 4 males, 4 females, each with associated pupal skin. WASHINGTON: Franklin County, Othello, 8 males, 10 females. Grant County, O'Sullivan Dam, July 1955, 3 males. WYOMING: Converse County, Boxelder Ck., S. E. Glenrock, 4800 ft., 5 July 1968, reared, 6 males, 4 females, each with associated pupal skin. Natrona County, Bates Ck., S. Casper, 5600 ft., 5 July 1968, reared, 8 males, 10 females, each with associated pupal skin. Park County, S. Crossing Cottonwood Ck., N. Cody, 5400 ft., 7 Aug. 1968, reared, 5 males, 10 females, each with associated pupal skin. Big Sand



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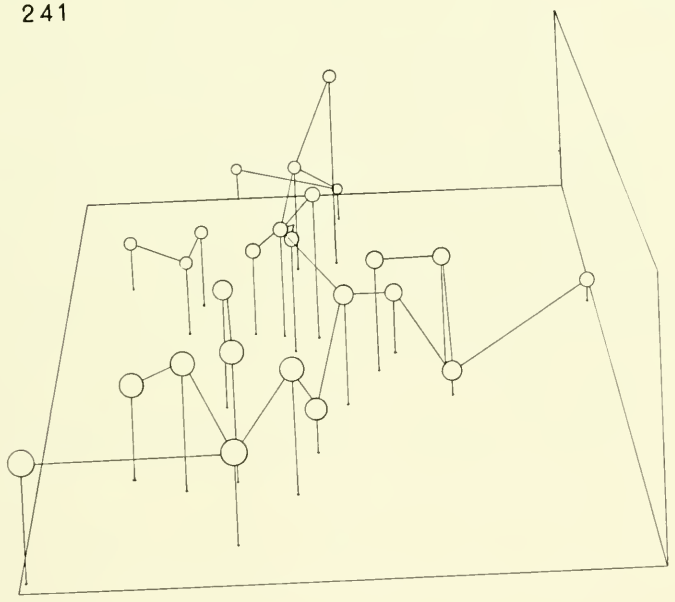


242

Fig. **241.** Projection of means of 25 samples of *C. (S.) jamesi* males onto the first three discriminant functions. The size of the balls implies distance from the viewer. For explanation of locality codes, see Table 18. Fig. **242.** Samples of *C. (S.) jamesi* as shown in Fig. 241, linked by the lowest value between pairs of samples in a generalized distance matrix.

Coulee, 13 mi. S. Belfry, 4000 ft., 7 Aug. 1968, 3 females with associated pupal skins. Platte County, N. Laramie River, 20 mi. N. W. Wheatland, 4700 ft., 4 Juy 1968, reared, 5 males, 8 females, each with associated pupal skin. 12 mi. N. W. Wheatland, 4700 ft., 4 July 1968, reared, 10 males, 15 females, each with associated pupal skin. Sublette County, Cottonwood Ck., 10 mi. S. Daniel, 7000 ft., 8 Juy 1968, 27 males, 23 females, each with associated pupal skin. Weston County, Stockade Beaver Ck., 2 mi. E. Newcastle, 4300 ft., 9 Aug. 1968, reared, 13 males, 19 females, each with associated pupal skin.

Dubious records: Khalaf (1957) reported this species from Goodwell and Nowata, Oklahoma; however, I have been able to examine only one specimen from each locality. These records are quite some distance from the nearest part of the general range of this species and may be mislabeled specimens. Therefore, further collecting will have to be done in these areas to verify Khalaf's records.

Statistical Analysis of Variation

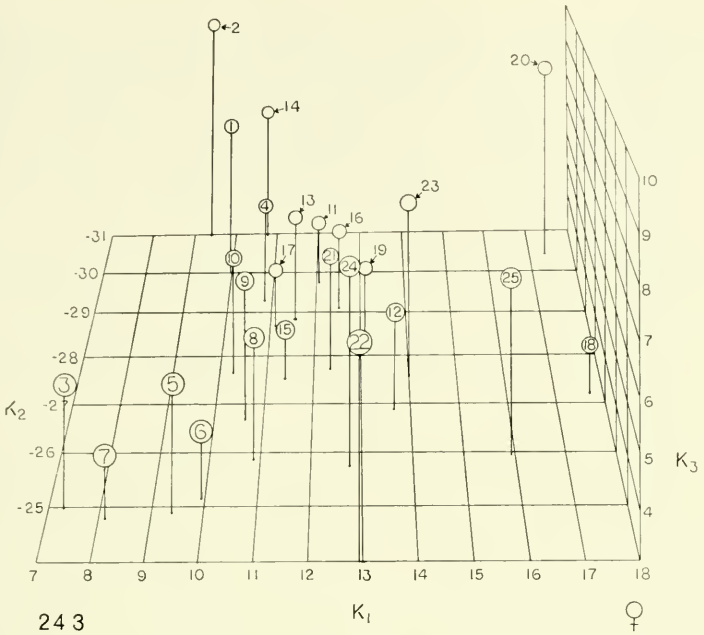
Analysis of variance of 10 male and 16 female characters indicate significant interpopulational variation in all characters at the $P<.001$ level. Means of characters by locality are given in Tables 18-20 and pooled within group variance-covariance matrices in Tables 21 and 22.

The partitioning of the roots in the discriminant matrix of 10 measurements on males gave a total variance of 1406.538. The first three components explained 81.68% of the variance and all 10 components were highly significant ($p<0.001$). In females, the discriminant matrix of 16 characters gave a total variance of 2035.876 and the first 15 components were highly significant, the 16th was nonsignificant. The first three accounted for 76.79% of the variance.

The projections of group means onto discriminant functions resulted in a rather amorphous assemblage of groups (Figs. 241, 243). In females, the southern Utah localities group together, with the exception of the Wayne #1 County sample, which appears to show more affinity to the northern Utah forms. Samples from Rosebud and Big Horn counties in Montana are misplaced with respect to the other northern localities, and in the generalized distance matrix are closest to locality #8, Garfield County, Utah. Four localities, Sublette and Park counties, Wyoming, Custer County, Montana, and Elko County, Nevada, tend to form a loose group. In nearly all characters examined, the Big Horn County, Montana, sample consistently falls near the southern Utah forms. The reason for this will become evident later.

Significance tests could not be performed on the samples of *jamesi* at this time, since the removal of a number of individuals because of missing data resulted in very small samples in several cases. The results of significance tests, therefore, probably would not represent the phenetic discontinuity of the data.

The set of vectors (Figs. 245-246) plotted for the first two discriminant functions shows trends in geographic variation for the characters examined



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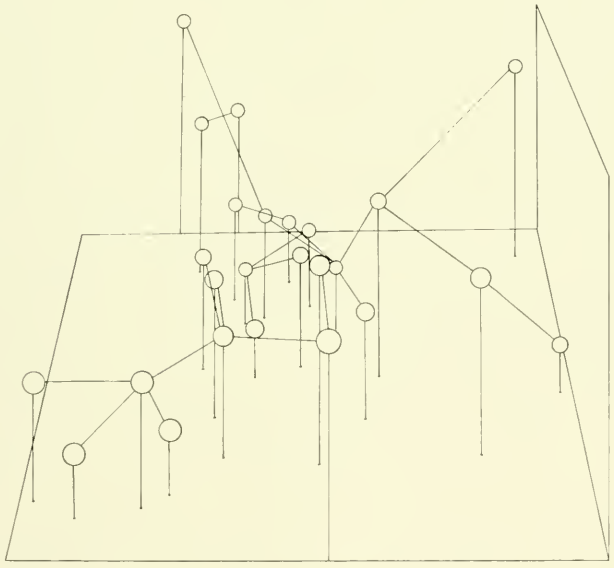

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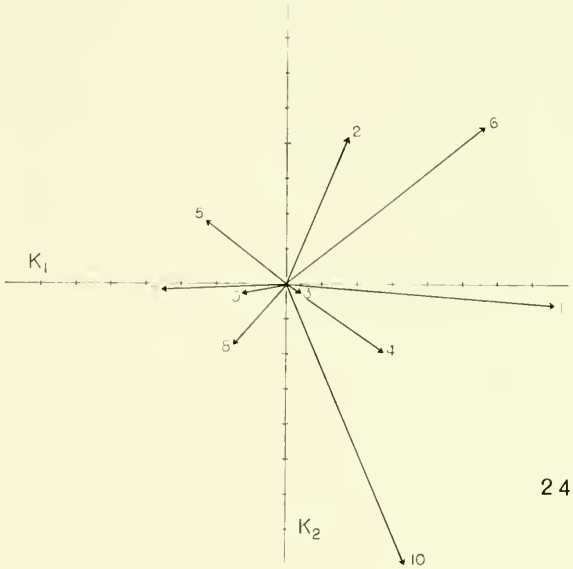
Fig. **243.** Projection of means of 25 samples of *C. (S.) jamesi* females onto the first three discriminant functions. The size of the balls implies distance from the viewer. For explanation of the locality codes, see Table 18. Fig. **244.** Samples of *C. (S.) jamesi,* as shown in Fig. 243, linked by the lowest value between pairs of samples in a generalized distance matrix.

when compared to Figures 241-244. Females with low K_1 and high K_2 values are smaller with a shorter wing, antenna, hind leg, head and fewer maxillary teeth, while those with low K_2 values have a longer wing, hind leg and antenna. Females from localities with high K_1 and K_2 scores have a longer third palpal segment and more maxillary teeth. Females from localities with high K_1 have the fewest antennal sensory pits, while those with low K_1 and K_2 have the most. Males with low K_1 and K_2 values are smaller with a shorter wing, hind leg and telomere, while those with high K_1 values have these parts longer. Males with high K_1 have the most antennal pits, while generally those with low K_1 and high K_2 have the least. Individuals in samples with low K_2 values have a broad telomere tip, those with high K_2 and low K_1 have a narrow tip, and the intermediate forms are spaced out in between.

In the principal components analysis, nine factors were extracted for the females, which explained 76.33% of the variance. The first three, plotted in Figure 247, accounted for 58.71%. Factor I is a "general body size" factor in the adults, with highest factor loadings on the length of the femur, tibia, wing and flagellum. Factor II is a "pupal bristle" factor with the lengths of *ad*, d_1 and d_2 possessing the highest coefficients, while III is an "*lpm* tubercle" factor, with highest loadings on the number of spiniform tubercles on the penultimate abdominal segment. The significance of the other factors is not so clear. The high factor loadings are distributed as follows: IV, number of antennal sensory pits, follows by the color of the pupal respiratory horn; V, number of apical spiracular openings on the horn; VI, width of the third palpal segment; VII, number of tibial spines on the hind leg; VIII, number of lateral spiracular openings on the pupal respiratory horn; and IX, number of multiple sensory pits on the antenna.

In males, nine factors were likewise extracted, which explained 75.71% of the variance. The first three, plotted in Figure 248, explained 52.37%. The highest loadings in factor I were the same as those in females, while II had highest loadings for pupal bristle *am*. Factor III was again an "*lpm* tubercle" factor, but the highest loadings were for shape of the *lpm*'s and number of semi-spiniform tubercles on the penultimate segment. In the remaining factors there are much higher loadings on one or two characters in each factor than was found in females. For factor IV these were the number of apical spiracular openings on the pupal horn and width of the horn tip; V, color of the horn and abdominal skin; VI, number of antennal sensory pits; VII, number of pupal abdominal segments with spiniform *lpm* tubercles; VIII, number of tibial spines and number of lateral spiracular openings on the respiratory horn; and IX, shape of the ninth sternum in the adults.

In the plot of the first three principal components, the relationship of some localities with respect to the others is different from that shown in the



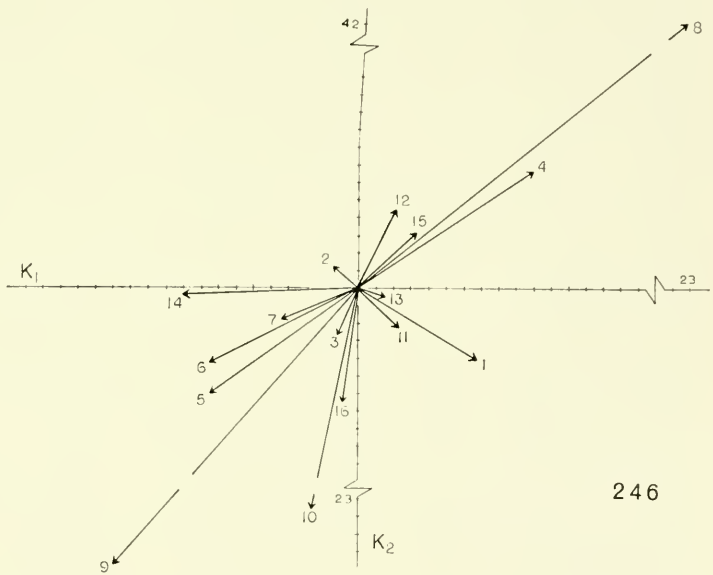


Fig. 245-246. Vectors for 10 characters of males and 16 characters of females of *C. (S.) jamesi* for the first two discriminant functions. Each vector shows the change in the discriminant function that the corresponding character would generate if it varied independently. For explanation of character codes, see text.

discriminant function analysis. Basically there are still three clusters, which are particularly evident in the females. The most obvious shift is in locality #7, Garfield County, Utah, which in the discriminant function and principal components analyses of females is close to localities 3, 5, 6 and 8; however, in the analysis of the males by principal components, this locality is distinct. There is also a shift in the Fremont County, Wyoming, locality, but, since this is such a small sample, little significance can be given the change.

A detailed discussion of the patterns of geographic variation in the pupae of *jamesi* can be found in Atchley (1970).

The analysis of geographic variation in *jamesi* is complicated by the presence of natural hybridization with *denningi* in the northern part of the range and with *hieroglyphicus* in the southern portions. This leads to difficulty in the explanation of trends in variation, which in some areas could be influenced by introgression of genes from a second species. This is discussed at some length in the section on natural hybridization.

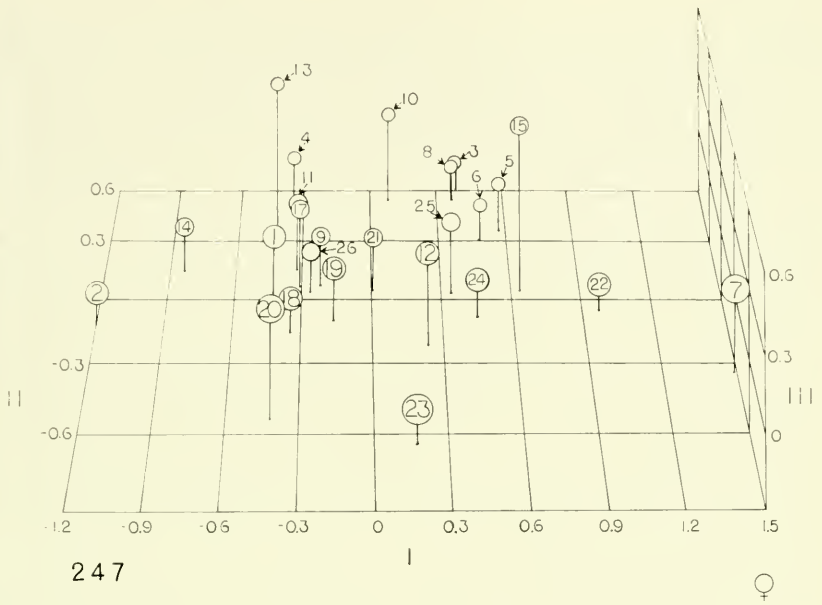
BIOLOGY OF THE IMMATURE STAGES

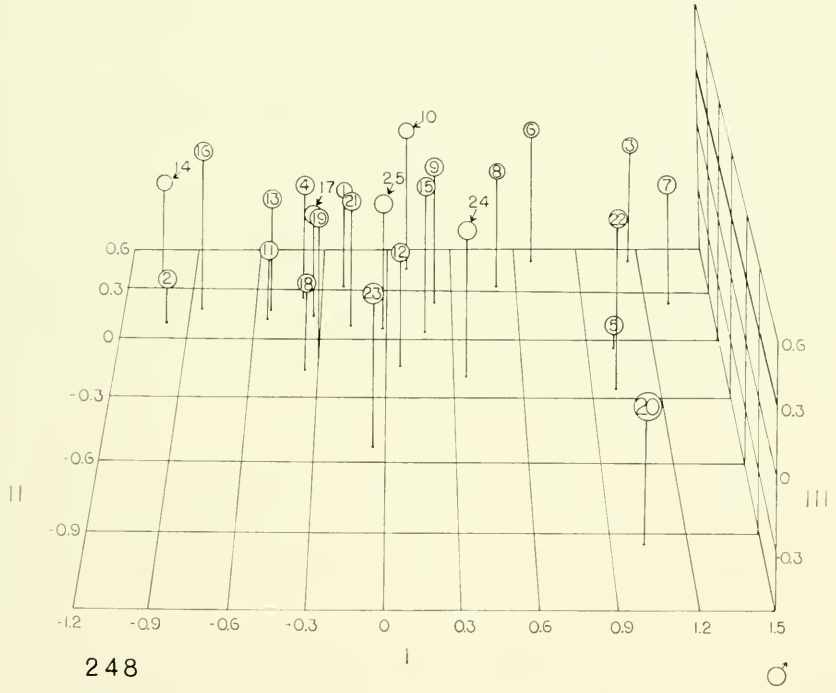
General Considerations and Methods of Study

Biological studies of the immature stages of ceratopogonids have long been hampered by the lack of adequate taxonomic studies of the larvae and pupae, as well as the difficulty of working with such small organisms. In spite of this, detailed studies have been made of the immature instars of a few species, utilizing various collecting methods.

Suspected breeding sites have been examined by means of box traps or modifications of these (Foulk, 1966), or even by bringing part of the habitat into the laboratory and rearing the immatures to adults in an emergence cage. These techniques, however, are of somewhat limited utility since they can be used only over small areas and yield only the adult flies. Often, in the cas of box traps, the soil is modified and emergence affected.

The extraction of larvae from soil is often a laborious task requiring washing and sifting. Simply placing part of the habitat material in a pan, flooding with water and stirring will yield some larvae, but usually at least an equal number are missed. In quantitative studies this method is not very effective. Therefore, various authors have sought to develop techniques that would give more representative numbers of larvae. Kettle *et al.* (1956) used a magnesium sulfate solution to separate larvae from soil samples, and more recently Davies and Linley (1966) have attempted to standardize this procedure for more reliable sampling of populations. Bidlingmayer (1957) used sand in place of magnesium sulfate for *C. furens,* but, as Kettle (1962) has pointed out, this method requires a positive response by the larvae,





Figs. **247-248.** First three principal components for 25 samples of *C. (S.) jamesi.*

which may vary from species to species, particularly in deep-burrowing forms.

The techniques just outlined are best used in close proximity to one's laboratory. They are impractical in large survey studies where ten or more localities may be examined in a single day in areas several hundred miles from permanent laboratory facilities. In these situations a quick method of surveying suspected habitats is needed. In this study, collections of immatures, particularly pupae, were made by scraping the top inch or so of mud from just above the water line into a white enamel pan, and then flooding the mud with water. Since pupae of the species of *Selfia* float, this made a quick and quite effective method for examining suspected habitats for this stage. However, in the case of larvae it is less effective since they often burrow back into the mud. One can usually obtain a sample of the species present, but large numbers can generally be obtained only by persistent collecting. The search for larvae can be facilitated by stirring the water in the pan, then pouring the supernatant into a second pan. The larvae are now usually easier to find, since the second pan contains mostly water and only a little of the substrate. Since the pupa was considered to be the most important of the immature instars in this study, and this was the most effective method for obtaining them, the loss of some of the larvae that might have been retained by the magnesium sulfate method was overlooked.

Pupae were pipetted from the water and isolated in vials containing a few millimeters of water and a strip of paper toweling and stoppered with a cotton plug. The pupae generally crawled up on the paper prior to emergence of the adult, and, after the adult was allowed to harden, it and the associated pupal exuvium were placed in alcohol. If larvae are available, they can be similarly isolated into vials containing a small amount of water and the larval exuvium collected after pupation. The use of a small, circular piece of sponge to simulate moist substrate, as described earlier (Atchley and Jackson, 1968), works very well with the larger ceratopogonids for which it was intended, but not for *Culicoides*. The smaller pupae of *Culicoides* often crawl down between the sponge and the wall of the vial, where they become trapped and drown.

Although rearing specimens according to this method is quite laborious, the results are well worth the effort. With accurately associated adult and immature instars, more refined taxonomic analyses are possible; in addition, meaningful studies of geographic variation-covariation between immature and adult characters are possible.

General Habitats of Culicoides

The family Ceratopogonidae is rather readily separable into two sections, one aquatic and one terrestrial, although some genera should probably be

considered as intermediate. That the family arose from some aquatic precursor can be judged from the respiratory system of the larvae. They are apneustic and consequently must derive oxygen from their surroundings by cutaneous respiration, a method associated with aquatic forms. The terrestrial forms, e.g., *Forcipomyia,* appear to have entered their habitats secondarily.

The high degree of morphological homogeneity among species of *Culicoides* belies a marked divergence in larval habitats among the many groups of species. These flies have radiated to occupy a diverse range of niches. The original habitat of the genus must have been large, permanent, more or less freshwater marshes, or swamps, not subject to periodic desiccation, inundation or other drastic environmental fluctuations.

From such a generalized habitat, *Culicoides* evolved in many directions. Some groups have grown progressively more tolerant of salt water and because of this and their biting habits are a source of annoyance near coastal marshes. Specialization has often been in the direction of smaller and smaller microhabitats. Examples of this can be found even in those species that breed in the broad expanses of coastal marshes. Hogue and Wirth (1968) recently described a new species living in crab holes but belonging to the *furens* group, common inhabitants of coastal marshes. Immature stages of two other species are known to utilize this unusual habitat.

As in other aquatic Diptera, *Culicoides* midges have invaded plant containers and rotting vegetation. In the United States, all of the species of the rather large *guttipennis* group except one have been reared from wet or moist tree or stump holes. Most of the *copiosis* group breed rather indiscriminantly in the necrotic parts of cacti and may have evolved from treehole breeding forms, as evidenced by the inclusion of two forms utilizing treeholes exclusively, while the *guttipennis* group includes one species reared from water in a pocket in saguaro cactus. Other plant habitats include rotting cocoa pods, water-filled bromeliads, and rotting banana or bamboo stumps (Williams, 1964). Several members of the subgenus *Avaritia* commonly breed in horse or cow dung, and one Japanese species has been reared from chicken dung.

There are two general surveys of larval habitats which encompass a large enough geographical area to offer a chance of demonstrating general patterns. Jones (1961b), in discussing the larval habitats of 29 species of *Culicoides* occurring primarily in Wisconsin and the southwestern United States, listed three principal habitat types, each with further subdivisions. These include: wet soil environments, including freshwater streams, rivers, lakes and marshes and alkaline or saline water situations; plant environments, including tree and stump holes and rotting cactus; and damp terrestrial environments, comprised of manure piles, rotting corn stalks

and haypiles. Of Jones' three main categories, the broadly stated first one, soil environments, yielded the greatest number of species of *Culicoides*. In a similar study of the British species, Kettle and Lawson (1952) listed six categories: oligotrophic acid boglands, eutrophic freshwater marshes, swamps, mudflats, salt marshes and dung. Some of these, such as mudflats, were further subdivided into those polluted by animal manure, etc.

Biology of Immature Stages of Selfia

The only published reference to the biology of the immature stages of *Selfia* is that of Jones (1961b), in which he recorded, in a general way, the larval habitats of three species: *hieroglyphicus, jamesi* and *multipunctatus*. During the years 1965-1968, I was able to rear six of the seven species of *Selfia* from over 50 separate localities, ranging from southern New Mexico and Arizona to central Montana. The only species I have not been able to study in the field is *C. tenuistylus,* a form restricted to California.

The larvae of *Selfia* are small, elongate, eucephalous and aquatic, not much different from those of other *Culicoides*. They move through the water by a peculiar, rapid, side-to-side lashing motion usually thought of as being "eel-like." Becker (1961) estimated that in mature larvae of *C. circumscriptus* the side-to-side movements occurred at about 550 per minute. Younger larvae, however, are more sluggish. The pupae of *Selfia* are not capable of prolonged swimming movements but are quiescent, generally restricted to the margins of stream, lakes and other moist habitats.

The larval stage is apparently the longest part of the life cycle. This is stated with some reservation, since recent studies by Jamnback (1961) have shown that, at least in the laboratory, the adults of *C. obsoletus* are rather long lived, some females living as long as 51 days.

Larvae of *Selfia,* as in other groups of *Culicoides,* normally burrow and feed at the bottom of small streams and ponds, but, unlike some other groups of Diptera such as mosquitoes, they pupate above the water line either on the substrate or in small burrows. Because of this method of pupation, there is a shoreward migration of the mature, fourth instar larvae, by swimming at or near the surface of the water, to the site of pupation and emergence. Therefore, larvae taken from the mud or sand along the shore will generally pupate in a short time, usually in a day or so.

The onset of pupation is evidenced in mature larvae by the appearance of the pupal respiratory horns beneath the larval thoracic cuticle, the retraction of the anal segment of the pupa inside the larval skin, expansion of the thoracic region, etc. Lawson (1951) has given a time sequence of the events leading to pupation in *C. nubeculosus,* and Becker (1961) has discussed similar events in *C. circumscriptus*. The exit opening for the pupa is apparently a dorsal split beginning in the prothoracic region, the

larval skin then being pushed posteriorly by the movements of the abdominal spines and lateral processes on the anal segment. Often in recently pupated individuals the larval skin and head capsule can still be found attached to the posterior segments of the pupa; however, the larval exuvium is soon lost.

The pupal stage in *Selfia* generally lasts from three to five days and is a period of little activity. At the time of emergence, the pupal skin splits, with the operculum becoming an outwardly projecting flap. The adult fly pulls itself free from the pupal skin and stands on the substrate for a short time in order to harden. Since the pupae are generally confined to the margins of streams and lakes, and, as in the case of other *Culicoides*, adults will not emerge if the pupae are covered by water, they have much less chance of drowning than do "aquatic" pupae, such as those of chironomids or mosquitoes. I cannot say definitely whether the pupae of the various species of *Selfia* lie on the substrate or in small burrows with only a little more than the respiratory horns protruding, as reported by various authors for species in other subgenera. There is some evidence that pupal burrowing occurs in *Selfia* (see section on *C. denningi*), but this will have to be ascertained in the laboratory.

Occurrence of the pupae in the marginal substrate probably in part accounts for the large numbers of ants, tiger beetles and other predaceous insects along the margins of streams and ponds where *Culicoides* are abundant.

Several factors affect the distribution and density of the immature stages along a given stream. Recognition of these would no doubt affect the results of studies where one is attempting to ascertain the relative population densities in different types of larval habitat. The pupae of *Selfia*, and apparently those of other stream inhabitating ceratopogonids, are not randomly distributed along the bank of a stream but rather are clumped at various points depending on the depth and amount of flow of the water. Pupae are generally most numerous along the banks of rather quiescent pools just below rapid water, or along bends in small streams. If one studies the movement of the water for a moment and observes where the action of waves might deposit a relatively nonmotile object, such as a pupa that had been washed off the margin, or where a larva might find it easiest to swim, then pupae will generally be most numerous at that point. On several occasions I have dropped pupae of some of the larger genera of ceratopogonids into stretches of turbulent water, and recorded where they came to rest. In most cases, after several trials the ultimate resting place was approximately the same. With a little experience one can usually learn to recognize those regions along a small stream that would yield the greatest density of pupae. This clumping pattern can also apply to large swift rivers. For example, the Green River at Dinosaur National Monument near Jensen, Utah, is a wide,

deep, swift river with strong marginal wave action. An hour of concentrated collecting along those areas affected by the strong wave action produced only a single larva and pupa. However, collection from a small, quiet, backwater about two feet wide and four feet long revealed large numbers of pupae. After thoroughly collecting this small area, I returned on two separate days and each time found numerous pupae in the backwater but again few along the margin proper.

The effect of wind on the microdistribution of larvae and pupae was also noted on several occasions, particularly when there was little marginal vegetation to serve as a windbreak. At several localities where a small quiescent pool was formed for any of several reasons, a wind brisk enough to cause slight waves on the surface resulted in a much higher density of pupae on the leeward side. Close scrutiny of each side of the pool revealed no discernible differences other than wave action to account for such unequal distribution. Apparently wind often functions like the rate of flow of a stream in concentrating pupae at certain places.

Probably wave action, either as a function of velocity of the stream or of wind, acts on the larvae rather than pupae. The larvae undergo their lateral migration generally by swimming on the surface of the water. Consequently, they would be affected by surface interaction with the waves and no doubt would swim in the direction of least resistance, resulting in the clumped distributions just described.

Wave action can also distribute pupae over a much greater area than is occupied by the larvae. Waves can wash pupae off of the margins and carry them for some distance before they are again able to make their way to the margin or vegetational areas where emergence can occur. In view of the limited vagility of the adult flies, this type of passive movement would have a marked effect on their distribution.

Wind and wave action must be taken into account when one attempts to ascertain the density of a species in a particular habitat. One might record slight breeding in a particular region, but a few yards downstream the density of larvae or pupae might be described as high due to clumping by wind or waves. The possible effect of soil type on the distribution of immature *Culicoides* is discussed later with regard to the biology of *C. denningi*.

One of the most important prerequisites for studying the biology of immatures of any species of *Culicoides* is the ability to recognize a potential larval habitat. Rather than list and describe each site from which a particular species was reared, I have discussed only those areas where breeding was dense and then tried to extract as many generalizations as possible from all sites of a given species in an attempt to make future recognition of the larval habitats easier. I have endeavored to describe the generalized habitat for each species, have given a photograph of such a habitat when possible,

listed any exceptional or unusual environments, and, when possible, discussed any factors which appear to be of importance in limiting the distribution of the species. In discussing environments or factors possibly limiting distribution, one must be careful to avoid spurious correlations. Since these flies are aquatic in the immature stages and the adult females are bloodsuckers, correlation of their distribution with a particular type of plant in the environment, for example, would probably only reflect the type of climate and not a particular requirement of the insect.

Many areas of the western United States and Mexico where the species of *Selfia* occur abundantly are notably lacking in water. As a consequence, aquatic organisms, such as larvae of *Selfia,* have had to adapt themselves to small aquatic situations, which are often few and far between, subject both to drying up and to inundation by flash flooding, or which are hot, unshaded and windswept, due to the paucity of vegetation. Where such sources of water are infrequent and small, they are often polluted by frequent animal visitors, such as cattle.

A. *Culicoides (S.) hieroglyphicus*

Culicoides hieroglyphicus is a common species in the southwestern United States and Mexico and has been taken rarely as far north as central Wyoming. I have reared this species from 13 different localities ranging from southern New Mexico to northern Utah. Five of these were classified as having moderately dense to dense breeding of *hieroglyphicus,* three as moderate and five as slight.

In nearly all cases this species was associated with small (less than five feet wide) to medium-sized, freshwater to alkaline streams. The only exception was a large collection from an arm of the San Juan River at Bluff, Utah, a large but rather slow moving river (Fig. 250). The stream margins at all localities were soft mud and/or sand, lacking marginal or shading vegetation. The heaviest breeding was encountered at a small alkaline wash a mile southwest of Cisco, Utah (Fig. 249). This stream was only about two feet wide in most places, had a soft mud bed and margin, warm water (temp. 31°C) and no vegetation. Here the immature stages were very dense, several hundred larvae and pupae per eight-inch square section of mud, and associated with slight breeding of *variipennis.*

Jones (1961b) reared *hieroglyphicus* from four localities, two in northern Oklahoma and two in the Big Bend region of Texas. The Oklahoma material was reared from the margins of lakes and apparently represented slight breeding. The Texts habitats included a mudflat, where moderately heavy breeding was noted, and the exit of a hot spring along the Rio Grande, which showed moderate breeding.

A number of physical and chemical attributes of the water are of possible significance in limiting the distribution of species of organisms with an

aquatic stage. One factor of apparent importance to *C. hieroglyphicus* is temperature. Of 12 localities from which data are available, all but two were warm streams with temperatures of 27°C or above. One of the exceptions was a small pond alongside Crooked Creek in Meade County, Kansas, which had a water temperature of 25°C and only slight breeding of *hieroglyphicus*. The other was Fremont River just below the visitor center at Capitol Reef Monument, east of Torrey, Utah, where the water temperature was 22°C. This locality will be discussed further.

On a few occasions I was able to follow a particular stream or river for a considerable distance and through several ecological zones. By doing this I hoped to find regions where two species occurred sympatrically and then, by moving up and down the stream, find the areas where each form occurred alone. This is of considerable significance not only in understanding the ecology of these flies but also in attempting to analyze possible introgressive hybridization. One such area was Fremont Creek in south central Utah.

Beginning at Hanksville, Utah (4200 ft.), I made four collections up the Fremont River as far as Bicknell (7100 ft.), a distance of 53 miles. At Hanksville and the second locality, 15 miles west of Hanksville (4900 ft.), the river was moderately large, 15-20 feet across, and flowing rather rapidly through a saltbush-greasewood association (Küchler, 1964). The water was warm (29°C), and *hieroglyphicus* was the only *Selfia* species present. The third locality, in a canyon just below the visitor center of Capitol Reef National Monument (5400 ft.), was more or less on the borderline between the saltbush-greasewood and Great Basin Sagebrush associations. Here the water was colder (22°C), and, although *hieroglyphicus* was still the dominant species, *jamesi* appeared for the first time, but only in slight numbers. Finally, in a juniper-pinyon woodland near Bicknell (7100 ft.), the creek was much smaller and colder (18°C), and only *jamesi* was present.

Woodbury and Musser (1963), in a limnological study of the Fremont River, showed a temperature fluctuation of only a few degrees in a 24-hour period at about the same date and locality as those of my collections. At the visitor center of Capitol Reef National Monument, they found the temperature to be 17°C at 5:30 p.m., while at 5:00 a.m. it was 15°C. Further, the velocity of the river at this locality (5400 ft.) was five feet per second, at 4800 feet it had slowed to 2.5 feet per second, and, finally, at 4600 feet the velocity was 1.15 feet per second. Their water temperatures at the various elevations closely approximate those recorded.

A little further south in Utah, similar procedures revealed the same type of altitudinal stratification. Although I was not able to follow the same river in this case, I was able to collect in the main stream and two of its smaller tributaries a few miles above it. Approximately equal numbers of *hieroglyphicus* and *jamesi* were taken from the Escalante River, 15 miles

Figs. **249-253.** Typical habitats for immature stages of *Selfia*. **249,** one mile S. W. Cisco, Utah, with dense breeding of *C. (S.) hieroglyphicus;* **250,** San Juan River at Bluff, Utah, producing dense breeding of *hieroglyphicus;* **251,** Willow Creek, 12 mi. N. Castle Gate, Utah, producing dense breeding of *C. (S.) jacksoni;* **252,** Big Sand Coulee, 13 mi. S. Belfry, Montana, showing darker colored sand islands (White strip equals six inches in length); **253,** Cottonwood Creek, 10 mi. S. Daniel, Wyoming, exhibiting dense breeding of *C. (S.) jamesi.*

east of Escalante (5100 ft.). Here the river was clear, rather rapid, about eight to ten feet wide, with sandy margins, no shading vegetation and a water temperature of 29°C. This is a juniper-pinyon woodland, but Küchler (1964) shows a saltbush-greasewood association just to the southeast. About 20 miles west of this locality two other collections were made at 6000 and 6600 feet in cold water habitats (temperatures 23° and 25°C, respectively). Only *jamesi* was present at each of these localities.

Two additional localities, in Kane County, Utah, and San Miguel County, New Mexico, support the hypothesis that *hieroglyphicus* is a lower elevation, warm water form that is replaced on an altitudinal gradient by *jamesi*. At both of these localities, collections from along a stream system or along an altitudinal gradient revealed *hieroglyphicus* common in the lower, warmer elevations and replaced by *jamesi* in the higher, cooler situations. The region of overlap in all four of these areas was between 5000 and a little over 6000 feet. The possibility that these two species replace each other along such an altitudinal gradient due to interspecific competition is very unlikely.

Late in the summer *hieroglyphicus* may appear at higher elevations, either as a result of being able to extend its range into the higher elevations with warmer weather, or a few larvae might overwinter there and delay emergence until late summer. I have found small numbers of *hieroglyphicus* in the high mountain regions of southern New Mexico in the later summer months and, likewise, in northern Utah. At Dinosaur National Monument, in northeastern Utah, collections in early July reveal only *denningi* and *jamesi,* the former species being most abundant, while in the latter part of August *hieroglyphicus* is most abundant, followed by *denningi*.

The idea that this species prefers warm water situations is substantiated by Jones' (1961b) rearing it in moderate numbers from a hot spring and my own collections of it from the hot springs region of Las Vegas, New Mexico.

Further studies of this species are needed along altitudinal gradients such as those described, but over longer periods of time in order to study the amount of seasonal fluctuation at the upper and lower limits of the gradients, particularly in regions where the distribution of *hieroglyphicus* overlaps that of *jamesi*.

B. *Culicoides (S.) jamesi*

Culicoides jamesi appears to have broader ecological tolerances than the other species of *Selfia*. I have found it in moderate numbers in small to large, freshwater, alkaline and polluted streams, with cold to warm water. I have reared it from 27 localities, ranging from northern New Mexico to central Montana: five localities with dense breeding, twelve with moderate and ten with slight.

Of the five localities exhibiting dense breeding, three were cold fresh-

water situations (water temperature 19°-21°C). Two of the cold water streams were small to medium-sized with rather rapidly flowing water, sandy margins and no shading vegetation. One of these, Stockade Beaver Creek, two miles east of Newcastle, Wyoming (4300 ft.), is located in a wheatgrass-needlegrass grassland (Küchler, 1964). Extensive collections made a few miles upstream from this locality, in a Black Hills pine forest at elevations of 4900, 5100 and 5300 feet, were negative for *jamesi,* but tremendous numbers of *variipennis* were present. At these stations the stream was flowing more rapidly, had clay-rock margins and colder water (16°C). The second cold water habitat, Cottonwood Creek, 10 miles south of Daniel, Wyoming (7000 ft) (Fig. 253), was a sagebrush steppe association. The third cold water collection was made from a small pond formed above a waterfall on Willow Creek, 12 miles north of Castle Gate, Utah (7600 ft.) (Fig. 251), in a Spruce fir-Douglas fir forest (Küchler, 1964).

Of the two warm water habitats (27°-30°C) where there was dense breeding, one was a small, shallow, freshwater stream at the outskirts of Mt. Carmel Jct., Utah (5300 ft.), in a juniper-pinyon woodland, and the other was rather unusual in that it was a small, very slowly moving, highly polluted creek 30 miles north of Volborg, Montana (2400 ft.). The water at the latter location was a greenish-yellow color and the margins were soft mud. This locality, in the Grama-needlegrass-wheatgrass grasslands of eastern Montana, supported large numbers of immature *jamesi* and smaller numbers of *denningi* and represented a hybrid zone for these two species.

An area was found about five miles west of Escalante, Utah, that afforded an unusual opportunity to examine different possible larval habitats within a very small area. Two large, cold water creeks, Upper Valley and North Creek, and several smaller streams run together there. The smaller streams were apparently of spring origin and flowed across a rather large mudflat before joining the two main creeks. This created two distinct types of stream habitat; one was rather large and deep with swift currents and margins of soft mud interdispersed with numerous rocks, while the other comprised several slow, quite shallow (about a foot wide and two to three inches deep), more or less meandering trickles flowing across a soft muddy flat. Numerous larvae and pupae were taken in this area; however, all were from the mudflat site and not from the more or less torrential creeks. Since immatures have been recovered from both habitat types at other localities, there are two possible explanations for this. The gravid females of *jamesi* can either distinguish between the two habitat types and have a preference for the mudflat, or the larvae, if present in the bottom mud of the swifter streams, could not swim to shore and were washed downstream. No larvae, however, were found in the mud at the bottom of either swift stream.

At present it is difficult to deduce any specific limiting factors for *jamesi,* although, as discussed for *hieroglyphicus,* there is apparently a temperature-elevation factor, with *jamesi* being confined to the higher, cooler areas, particularly in the southern portion of its range.

C. *Culicoides (S.) denningi*

Present records indicate that *C. denningi* is restricted to northwestern United States and western Canada, occurring down the Rocky Mountains as far south as Garfield County, Utah. I have reared this species from 16 localities, ranging from south central Utah to central Montana, including two localities with dense breeding, five with moderate, and nine with slight. This species appears to have a little broader ecological tolerance than its sister species, *hieroglyphicus,* but probably not as broad as that of *jamesi.* I have reared it from large as well as small, cold to warm streams containing fresh or polluted water.

Of the two localities with dense breeding, one was a wide, swift, deep river in northeastern Utah, the Green River (4500 ft.), which was discussed earlier in the general comments section. This is a cold river (temperature 23°C) in a saltbush-greasewood association. The only other record of dense breeding was from a small, clear, moderately flowing stream with gravelly margins, the North Fork of the Humbolt River, about 16 miles northeast of Elko, Nevada (5200 ft.). This is a cool stream (25°C) in a Great Basin Sagebrush association.

Culicoides denningi was also reared from habitats ranging from the very cold (17°C), swift, Sevier River in Garfield County, Utah (7100 ft.), to a small, hot (33°C), stagnant stream at the outskirts of Delta, Utah (4700 ft.), where the marginal mud a few inches above the water level lay dried and cracked open. In both these extremes, *denningi* occurred in moderate numbers. In a polluted stream north of Volborg, Montana, discussed briefly under *C. jamesi, denningi* occurred in slight numbers.

One might question whether the type or texture of the marginal substrate would affect the microdistribution of pupae. In at least one instance this was found to be true. Collections from Big Sand Coulee, a rather small, relatively clear stream 10-15 feet wide with a rock and sand-mud bottom, 13 miles south of Belfry, Montana, revealed very disproportionate numbers of pupae from two types of soil. There was evidence of recent higher water, which had apparently produced small islands of sand an inch or two from the water's edge interspersed in soft mud (Fig. 252). Mud separated the sand islands both from the water and from other islands, which were only a few inches away. By carefully removing the top half-inch to inch of sand from the islands and comparing it with equal amounts of the intervening mud, I found there were about seven pupae on a sand island to one in a comparable amount of mud.

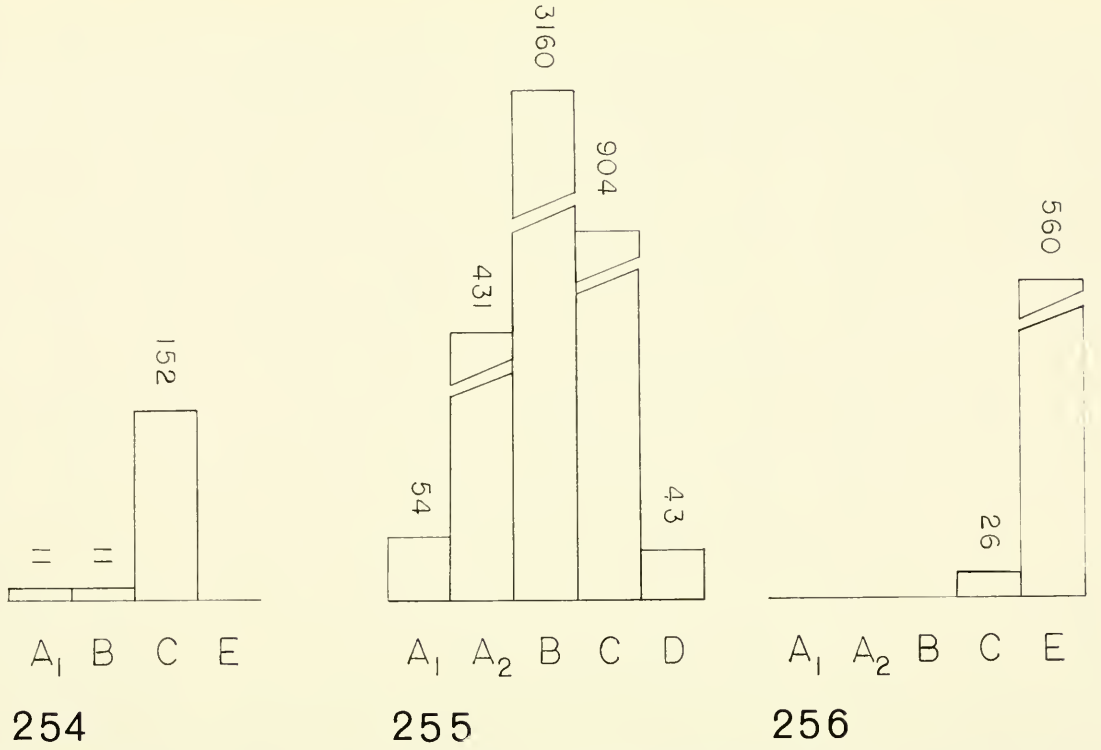
Linley (1965) found that three different types of soil had no effect on the larvae of *C. furens;* therefore, these observations raise several interesting, but still unanswered, questions. Since there was moderate breeding of *denningi* and slight breeding of *jamesi* along this stream, there may be a species specific response by the larvae to different types of substrate, with *denningi* found in the sand islands and *jamesi* in the mud. At present, this would not seem to be the case; however, a conclusive answer can be reached only by laboratory studies, since the specific identity of the pupae would be very difficult to determine in the field. The compactness of the substrate could account for such disproportionate numbers of pupae in the sand and the mud. Since the sand along the bank was less tightly packed and might be easier to burrow into than the mud, the larvae could be preferentially migrating to the sand because of a burrowing behavior either by the larvae prior to pupation, or the pupa immediately afterwards.

Linley's work on the behavior of the larvae and pupae of *C. furens* has shown that the larva of this species makes a small burrow in which pupation occurs and where the pupa generally remains until emergence. Megahed (1956) described the partial burial of pupae in *C. nubeculosus,* while in *C. circumscriptus* burial is almost complete with only the tips of the respiratory horns above the surface (Becker, 1961). Lutz (1912), however, found the pupae of *C. reticulatus* lying on the surface. Becker was able to show that in *C. circumscriptus* it was the pupae and not the larvae that did the burrowing. Such burrowing behavior is unknown in most other species due to the lack of detailed studies.

Therefore, with respect to the two species of *Selfia,* there may be either a species specific response of the larvae to different types of substrate, or possibly a differential response by the larvae of both species to sand rather than mud because of burrowing behavior. Since there was evidence of recent higher water, a third possibility might be that the larvae swam to the sandier margins when the water level was higher, and, since the water had receded, no lateral migration had occurred. There is no evidence to support this.

A recent paper by Fredeen (1969) on the biology of *denningi* supports a number of my suppositions. Fredeen has examined the biology of the immature stages of *denningi* over a period of several years in the South Saskatchewan River, a large river 200 to 600 meters wide and with mid-channel depths of one to ten meters. The river bed is composed of quartz sand and lacking in vegetation except for algae. He found *denningi* occurred for a distance exceeding 1100 km. along the valley of the South Saskatchewan, but not in the North Saskatchewan.

Fredeen has substantial evidence of a disproportionate horizontal density of larvae in the river depending on their age and the proximity to time of



FIGS. 254-256. Horizontal migration of *C. (S.) denningi* larvae in the South Saskatchewan River (from Fredeen, 1969). **254,** four weeks prior to period of maximal pupation; **255,** period of maximal pupation; **256,** immediately prior to freeze-up of river. A_1=larvae collected in area on shore, not previously flooded; A_2=on shore, previously flooded; B=on shore, along margin of water; C=in river, 3 meters from shore under 0.5 meters of water; D=in river, 10 meters from shore under 1 meter of water; E=at mid-channel, approximately 180 meters from shore.

maximal pupation. Four weeks prior to pupation larvae were sparse at mid-channel, and near the margin the greatest larval density was about three meters from shore. At the time of maximal pupation, large numbers of larvae (3000 per m^2 in the top inch of sand, 645 per m^2 in the second inch) were found on shore along the margins, but considerably smaller numbers (30 to 40 per m^2) 10 meters out from shore. Just prior to freezing of the river, no larvae were found along the margin, a few three meters from shore, and large numbers at mid-channel (see Figs. 254-256 for summary). The South Saskatchewan River is ice-covered from early November to April, and *denningi*, as most *Culicoides*, overwinters as larvae.

Fredeen noted that the larvae swim toward shore on or near the surface of the water, and, upon reaching shore, quickly burrow into the sand tends to support the idea that the disproportionate numbers of pupae in two types of soil discussed earlier result from a differential response of the larvae, at least in *denningi*, to different soil types. During periods of quiet water, the migrating larvae produced a distinctive shimmering effect on the surface by their swimming motions. The effect of wind on the distribution of pupae was also noted and is in agreement with earlier statements in this study.

D. *Culicoides (S.) jacksoni*

Culicoides jacksoni has been reared from only two geographically disjunct localities, one in southern New Mexico and the other in northern Utah. This, together with a single locality in southern Arizona, represents the known distribution of the species.

The habitats at the two localities for immatures share several common features. Both are high elevation needleleaf forests, the southern New Mexico population from Cedar Creek Canyon near Ruidoso (7100 ft.) in a pine-Douglas fir forest and the Utah population from Williow Creek, 12 miles north of Castle Gate (7600 ft.) in a Spruce fir-Douglas fir forest (Fig. 251). These collections were made from cold water pools or ponds above a waterfall. The New Mexico population was in a very small, shallow, cold pool (18°C) formed by a small artificial earthen dam. Cedar Creek is a small stream, usually only a foot or two wide, with rapidly flowing water and a considerable amount of low weedy vegetation along the margins. Dense breeding of larvae and pupae was evident in the mud at the edges of the pool. Several hundred yards upstream, where several small streams entered Cedar Creek, a number of small ponds had formed immediately above or below small waterfalls, and the margins of these also contained larvae and pupae of *jacksoni*.

At the Utah locality, the stream is considerably larger, but the habitat of *C. jacksoni* agrees in most details with the Cedar Creek habitat.

This species, as indicated by its distribution, is adapted to rather cold

temperatures. At the New Mexico locality, for several nights before and after these collections were made, the temperature was in the low 30's. Further, in this area, *jacksoni* would appear to be a late spring and early summer form; in several different years I have not encountered this species past late June at this locality. It is usually most abundant in late May or early June.

E. *Culicoides (S.) brookmani*

I have reared *C. brookmani* from only two localities, Oak Creek at Sedona, Arizona, and Sycamore Canyon, 26 miles west of Nogales, Arizona. The Sedona locality was a small, shallow, algae-choked stream with slow moving water and soft, red sandy-mud margins, running alongside and finally joining, Oak Creek. There was low weedy vegetation along the stream. This habitat produced large numbers of pupae but no larvae. The pupae, although distributed all along the muddy margins, were more numerous in areas shaded by large trees.

At Sycamore Canyon, very slight breeding of this species was detected along a small intermittent stream. The stream, although containing permanent water, ran for short distances, then went underground only to reappear a short distance away. This produced small isolated pools in a sandy stream bed.

The pupae of *brookmani* appear to use their very unique respiratory horns as a floating device, apparently assisting their normal buoyancy. These structures, which contain numerous tracheal tubes, are slightly cupped at the apex; consequently, the vertical dorsal spiracular openings are out of the water when the pupa is floating.

F. Culicoides (S.) multipunctatus

Although I have reared this species from only a single locality in southern Kansas, Jones (1961b) found it rather common in Texas and New Mexico. The Kansas specimens were reared from a small pond formed along Crooked Creek, about three miles from Meade County State Lake. The pond lacked vegetation except for a few cattails, had gravelly sand margins, with a stratum of black mud about an inch below the sand surface. Only slight breeding of *multipunctatus* was noted.

Jones (1961b) recorded *multipunctatus* from a number of localities, including polluted as well as fresh water. These included lake margins, stock tanks, stream margins and flood-water pools along rivers.

G. *Culicoides (S.) tenuistylus*

The only reared material of this species has been collected by J. R. Anderson at Hopland, California, and was from the sandy margins of a stream. No other information is now available.

BIOLOGY OF THE ADULTS

With the exception of biting records, little information has been gathered on the biology of the adults. This information is summarized for each species.

A. *Culicoides (S.) denningi*

Biting records of this species indicate it restricts its feeding to large mammals. Fredeen (1969) regards horses as the principal host, but man is often severely attacked, at least in the Saskatoon area. As in many other species of the genus, *denningi* is crepuscular, its first biting period beginning shortly before sunset, and a second period just before sunrise. On cloudy days, however, it may bite throughout the day. I have recorded *denningi* biting man at several localities in Wyoming and in North and South Dakota.

B. *Culicoides (S.) hieroglyphicus*

I have never taken this species biting man, in spite of spending a considerable amount of time in areas where it was abundant. In the USNM collection there are several specimens that were collected biting jackrabbits. Jones (1961c) reported it attacking sheep; however, I have not seen these specimens, and they may be *denningi*.

C. *Culicoides (S.) jamesi*

There are no references in the literature to the host preferences. I have seen a few specimens collected from horses in northern New Mexico. I collected large numbers swarming around two persons at Lake Como, near Hamilton, Montana. One person was fair skinned, the other more darkly complected. The flies were considerably more numerous around the former than the latter, swarming about the head and face, crawling through the hair, etc., and were most active at dusk. In spite of the large numbers of gnats attracted, actual biting was never observed.

D. *Culicoides (S.) tenuistylus* and *C. (S.) brookmani*

In the USNM collection, there are ten females of *tenuistylus,* taken from the ears of deer, and two from jackrabbits, and three females of *brookmani* taken from deer and one from the ear of a jackrabbit, by Dr. J. R. Anderson, at Hopland, California.

The hosts of *C. (S.) multipunctatus* and *C. (S.) jacksoni* are unknown.

NATURAL HYBRIDIZATION

A number of populations of three species exhibit several rather peculiar patterns of variation not correlated with the usual trends shown earlier in this paper. These variation patterns are a result of natural hybridization among *hieroglyphicus, denningi* and *jamesi*.

Hybridization between biological species can best be shown either by cytological elucidation of choromosomal non-homology of parental chromosomes during the pachytene stage of meiosis, disruption of normal chromsomal mechanisms leading to gamete formation, or the reduction of fertility demonstrated in laboratory crosses. Recently it has been shown (Atchley and Jackson, 1968; Atchley, unpublished data) that pachytene studies and other cytological endeavors of any magnitude are virtually impossible in *Culicoides;* further, laboratory crosses necessitate colonization, which is very difficult with these flies, owing to host preferences and other factors. Consequently, at least for the present, studies involving hybridization in *Culicoides* must be based on morphology. The morphological demonstration of hybridization is theoretically well founded since phenetic characters are a direct or indirect expression of an individual's genotype and any change in the genotype, e.g., by hybridization, would be expected to be reflected by a corresponding phenotypic alteration. The ultimate analysis of species differences, as well as species barriers, however, will have to be obtained by artificial hybridization, followed by genetic studies of the F_1 generation and its progeny, if any are produced.

Some axioms regarding hybridization

Hybridization has been defined in many ways and at various levels, depending on the problem under discussion. Some geneticists, for example, have used the term to explain crosses between organisms differing by alleles at a single locus, while others have defined hybridization as the crossing of "genetically unlike" individuals. Neither of these definitions is very useful in an evolutionary sense, because, according to them, almost all sexual reproduction constitutes hybridization. A more useful definition refers to hybridization as "the crossing of individuals belonging to separate populations which have different adaptive norms" (Stebbins, 1959). This is broad enough to include interbreeding of species or subspecies.

The morphological recognition of hybridization must necessarily operate on the hypothesis that morphological differences between species depend on multiple factors rather than single genes and, for the most part, there is relatively little dominance. Further, the intermediacy of separate characters will be correlated, i.e., hybrids intermediate in one character will tend to be intermediate in others. Consequently, under these assumptions, a hybrid individual would be expected to be intermediate between its parents in most characters, and the greater the number of characters that can be found to be intermediate between putative parents, the higher the probability of an individual's hybrid origin.

The weak link in this hypothesis lies in the assumption of no gene interaction. The interaction of genomes from different species may produce

dominance, epistasis, etc., resulting in F_1 individuals which are phenetically more similar to one parent or the other. Stebbins (1950) has pointed out that in experimental studies in plants, the phenotypic appearance of the hybrids may differ considerably from what one might predict on *a priori* grounds. Ramon (1968), in a critical phenetic study of several taxa and hybrids of known genetic history in the composite genus *Haplopappus,* found that some interspecific hybrids were phenetically more similar to one or the other parent, indicating dominance in some parental characters. Similar results have been obtained by Heiser *et al.* (1965), Torres (1964) and others.

The practical significance of dominance in parental characters of hybrids is as follows. If the taxa undergoing hybridization possess a number of distinctive attributes allowing them to be easily distinguished in the pure state, the effects of dominance of some parental characters on the appearance of the offspring might not be very severe, since hybrid individuals could probably still be rather easily detected by other characters in which dominance is absent. If, however, the taxa were very similar, as in *Selfia,* and only a few structures differentiate between them, the occurrence of dominance in one or more of these characters would seriously hinder the elucidation of interbreeding. Because of dominance, the hybrid individuals might simply be thought to be slightly more variant specimens of the parental species. Further, the distinction between backcross F_2 individuals and F_1 individuals exhibiting dominance in some characters would be very difficult, if not impossible. Goodman (1967) has shown a statistical method for detecting backcross individuals, but to be effective *a priori* crosses should be made to determine the appropriate phenotypes. If dominance is lacking in an interspecific cross, however, the F_1 progeny will generally be phenetically intermediate and have a more or less uniform phenotype, while the F_2 and later generations will be highly variable.

The correlation of parental characteristics in the F_1 and F_2 generations is due to linkage and developmental correlation in gene action. In *Culicoides,* for example, the haploid choromosome number is three (Atchley and Jackson, 1968) and, therefore, if a charater is controlled by three or more genes, a high probability exists that linkage is present. Although such linkage combinations are generally broken up in later generations, they have a marked effect on the distribution of variables in the F_1 and F_2 generations. The breaking up of these linkage combinations in the F_2 and later generations results in highly variable individuals with many different morphological recombinations.

The progeny of most natural interspecific hybrids are far more likely to be backcross types than true F_2 segregates. The partially sterile progeny resulting from natural interspecific hybridization have a much greater

chance of producing offspring with the more numerous and viable parental species than with the much rarer and only partially viable F_1 individuals that may be present. It is this process that makes possible introgression of genes from the gene pool of one species into that of another.

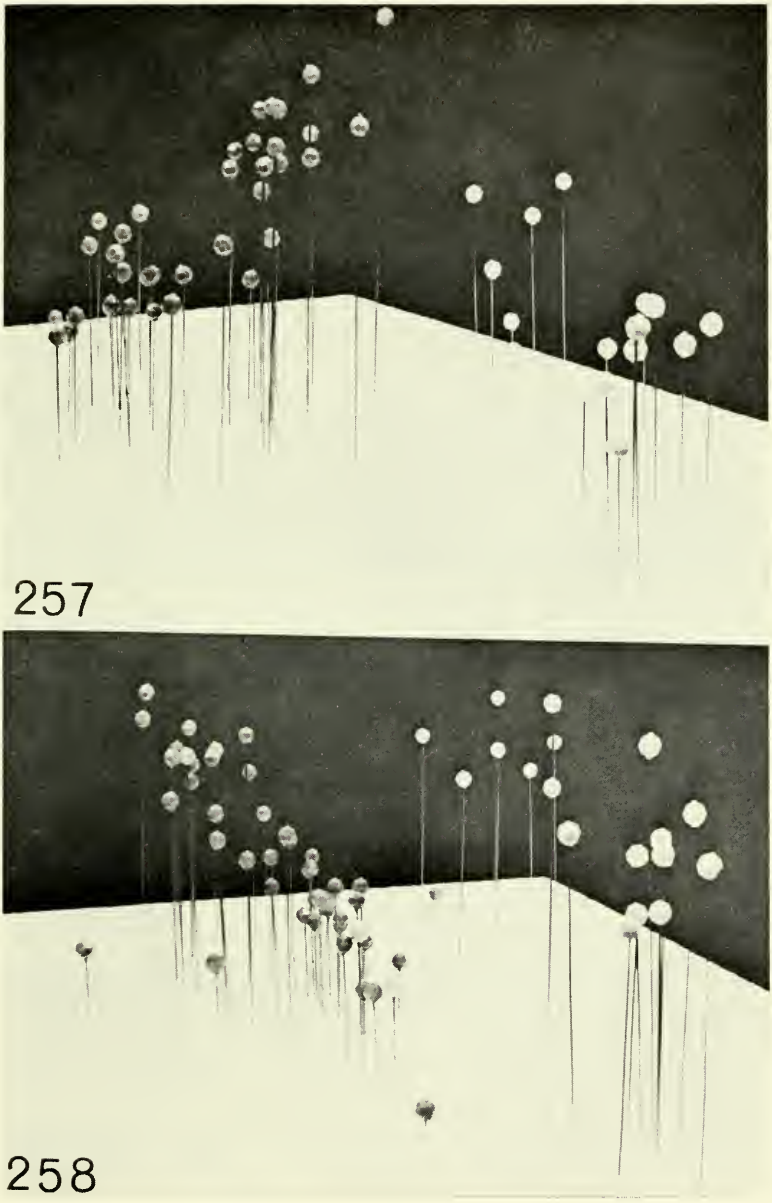
It became evident during this study that in *Selfia,* at least, before one can assume that individuals were hybrids if they possessed morphological characters which are seemingly intermediate between the conditions normally exhibited by two species, some information about patterns of geographic variation was mandatory. It is possible that in zones of overlap, polarity of morphoclines could mimic hybridization. For example, assume two good biological species, *X* and *Y,* where each possessed a different state of character *a* so that $X_{a'}$ and $X_{a''}$ are the normal conditions in regions of allopatry. As a result of selection for adaptation to changing environmental conditions, e.g., clinal variation, a shift from $Y_{a''}$ to $Y_{a'}$ could occur in a given population. If this were to occur in a region where *X* and *Y* overlapped, and, if there were very few distinguishing features to separate the two taxa, one might be led to believe hybridization was occurring. This is particularly true if there were one or more other clines behaving in a similar fashion. The ramifications of this situation are further discussed later in this section, with an example from *Selfia.* An example of a similar situation has been reported by White and Key (1957), who demonstrated cytologically that what appeared morphologically to be hybrids in grasshoppers were, in fact, only morphological deviates of two genetically well-defined species.

This brief discussion illustrates some of the difficulties associated with demonstrating natural hybridization on the basis of morphology. As far as possible these difficulties have been circumvented in the following materials; however, it must be admitted that, although hybridization is strongly indicated, the definitive proof requires laboratory synthesis of hybridization. This is true for any instance of morphological analysis of hybridization.

Hybridization between C. jamesi and C. denningi

At several localities in Wyoming, Montana, Nevada and Utah, a natural zone of hybridization between *C. jamesi* and *C. denningi* exists. Material at hand indicates the hybrid zone includes Big Horn, Custer and Rosebud counties in Montana, Park and Elko counties in Wyoming, Uintah County in Utah, and possibly two localities in Washington. One locality, Sublette County, Wyoming, will be discussed later.

Samples from four of these hybrid localities were compared with "pure" stock of each species by principal components analysis. The first three factors for males and females are shown in Figures 257 and 258. The "pure" stock was comprised of individuals from populations away from the hybrid zone. Components I-III in males explained 69.65% of the variance, and factor I was a "general body size" factor, II, an "*lpm* spine" factor, and III,



Figs. **257-258.** Principal components analysis of "pure" and hybrid populations of *C. (S.) jamesi* and *C. (S.) denningi*. **257,** males; "short" black balls at far left are pure *jamesi* stock; "short" white balls at right are pure *denningi* stock; center row of generally taller black balls are hybrids. Color of balls was determined by whether specimen had predominantly *denningi* or *jamesi* genitalia (see text). **258,** females; "tall" black balls at far left are pure *jamesi* stock; "tall" white balls at far right are pure *denningi;* "short" balls in center are hybrids. Color of ball for hybrid individuals based on discontinuous pupal characters (see text).

FIG. 259. Principal components analysis of females from "pure" and hybrid populations of *C. (S.) jamesi* and *C. (S.) hieroglyphicus*. White balls are *hieroglyphicus;* dark balls are *jamesi*. Hybrid individuals are four white balls between two clusters and two white balls in the cluster of dark balls.

a "d_2 bristle length" factor. Factors I-III in females explained 70.14% of the variance, and the factor loadings were the same as for males.

The black balls in the illustrations of the first three principal components are pure *jamesi* or hybrids with primarily *jamesi* genitalia or the discontinuous pupal characters of that species. The white balls are *denningi* or forms with predominantly a *denningi* genitalia or the discontinuous pupal characters of *denningi*. (Only two colors of balls were used because of lack of contrast in black and white photographs when more than two colors are used.) In the males (Fig. 257), the shorter black balls at the far left are pure *jamesi* stock, the shorter white balls at the far right are pure *denningi* stock and the center row of taller balls are hybrids. In females (Fig. 258), the shorter balls in the center of the model are the hybrids.

In order to obtain a more critical assessment of the hybrid individuals, a discriminant function analysis was performed on the "pure" samples of these two species, using the characters employed in the principal components study.

As mentioned earlier, principal components are very useful as a summarization procedure, in this case to demonstrate the occurrence of intermediate forms between the two species. However, subsequent analyses of the characters themselves is rather difficult. For this, discriminant functions are useful, although they cannot be used to show the existence of hybrids among non-hybrid individuals in a given sample, since this procedure discriminates *between groups* and obscures within-group variation. Consequently, the procedure outlined here was considered to be more efficient. If discriminant functions are used to separate two taxa, the result is a one-dimensional score, rather than a bivariate scattergram. The efficiency of this technique in separating the taxa is determined by the polarity of the clusters, since the specimens of one taxon should be clustered near one end of a frequency histogram, those of the other taxon at the other end. Subsequent inclusion of F_1 hybrids should form a third group about midway between the parental clusters.

Analysis of non-hybrid specimens of *jamesi* and *denningi* shows, as was expected, that a number of pupal characters will separate these species, but only a few from adult females will do so. The ultimate choice of an appropriate subset of characters was made on the basis of two criteria: (1) the magnitude of the coefficient of discrimination; and (2) the apparent multifactorial inheritance of the character. In hybrid studies, the use of characters controlled by numerous genes is more desirable than oligogenic ones since the more complex the genetic basis of a given character, the less likely the possibility that the offspring will show one or the other parental conditions.

Seven characters (one adult and six pupal) were chosen and with their coefficients comprised the following expression:

$$R\,♂ = 8.84(X_1) + 2.10(X_2) + 2.31(X_3) + 2.48(X_4) - 1.15(X_5) + 2.08(X_6) + 2.69(X_7)$$

$$R\,♀ = 0.37(X_1) + 1.32(X_2) + 4.00(X_3) + 2.10(X_4) - 4.00(X_5) - 2.85(X_6) + 4.92(X_7)$$

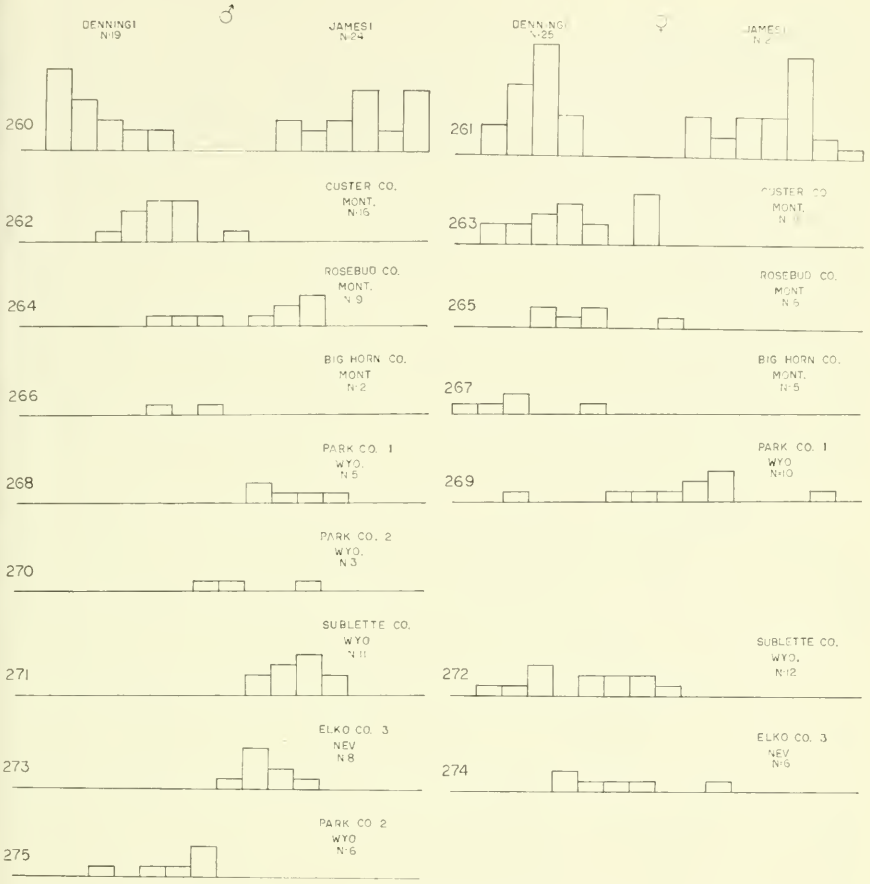
In males X_1 was the apical width of the telomere, while in females it was the sum of antennal sensory pits on both antennae. The remaining pupal variables were the same for both sexes and are as follows: X_2, length of the pupal respiratory horn; X_3, length of spine *am*; X_4, extent of the opercular cleft measured from the base of the *am* spine to the apicalmost extent of the submesal cleft in the pattern of opercular teeth; X_5, length of spine *ad*; X_6, length of spine d_1; and X_7, length of spine d_2. The mean discriminant function scores for 44 male specimens of *denningi* and 77 *jamesi* was 852.9 and 1352.1 respectively. In females, 49 *denningi* had a mean score of 510.5 and 100 *jamesi* specimens had 630.6 for these seven characters. As seen in

Figures 260 and 261, these character combinations effected a good separation of the two species in three "pure" populations from near the hybrid zone. The reason for exclusion of a number of characters of the male genitalia will be given shortly.

Three pupal characters were considered apart from the continuous variables used to prepare the discriminatory equation: the number of lateral spiracular openings on the respiratory horn and the shape and number of spiniform *lpm* tubercles on the abdomen. These structures are very efficient discriminators in the separation of *jamesi* and *denningi* and, consequently, have very large coefficients of discrimination. Segregation of these discontinuous variables, particularly the number of spiracular openings, does not necessarily follow the same pattern as shown by continuous variables such as spine length. Further, there is preliminary evidence that the genetic mechanisms underlying the expression of the number of spiracular opnings may not be as complex as in the quantitative characters used in the above equation. These discontinuous characters served an important role of providing a means to identify hybrids when dominance in the continuous variables or backcrossing might have caused them to be mistaken for normal *denningi* or *jamesi* specimens.

In the Custer and Big Horn samples, the continuous variables show the effects of hybridization by expression of phenotypes more or less intermediate between the parental forms; however, the number of spiracular openings generally does not deviate from the condition found in pure *jamesi* specimens. Further, in several of the hybrid swarms there is often asymmetry, with three openings on one horn and two on the other. Such asymmetry is absent in "pure" populations of these two species.

An explanation for the first phenomenon is simpler than for the second. The predominance of the *jamesi* pattern of spiracular opening in hybrids can be explained on the basis of simple genetic control of the number of openings with dominance in the hybrids toward the *jamesi* condition. The rather high frequency of individuals asymmetrical for number of spiracular openings is apparently due to the effects of gene penetrance. In individuals heterozygous for the genetic mechanism controlling the number of openings, i.e., hybrids, the internal environment created by the presence of two different genomes may cause a variation in phenotypic expression, therefore, producing the asymmetrical pattern. Evidence for this is found in hybrid individuals with three lateral branches from the trachea in the horn but only two openings, or individuals with the proximal two openings in the normal position, but the third lying just below the apex of the horn. The correlation between penetrance and expressivity of genes is quite complex, and the reader is referred to Strickberger (1968) for a more detailed discussion.



Figs. **260-261.** Discriminant function scores for "pure" samples of *C. (S.) denningi* and *C. (S.) jamesi* based on seven pupal and adult characters. Figs. **262-274.** Discriminant function scores for seven hybrid populations based on seven pupal and adult characters. All had some or most of the discontinuous characters of *C. (S.) jamesi* (see text for explanation). Fig. **275.** Discriminant function scores for hybrids from Park County, Wyoming, which had male genitalia predominantly of *C. (S.) denningi.*

Many characters of the male genitalia could not be used again because of the very large coefficients of discrimination. As in the discontinuous pupal characters, the inclusion of genitalia features with their large coefficients often obscured the relationship as shown by a number of continuous variables. The genitalia characters were used to identify hybrid individuals in cases where dominance in the discontinuous pupal characters might lead to confusion. The exclusion of genitalia characters from the discrimination function equation was not thought to have an effect on the analysis since the seven characters used in the equation gave very similar results to those

obtained when a large suite of adult and pupal attributes were examined by principal components.

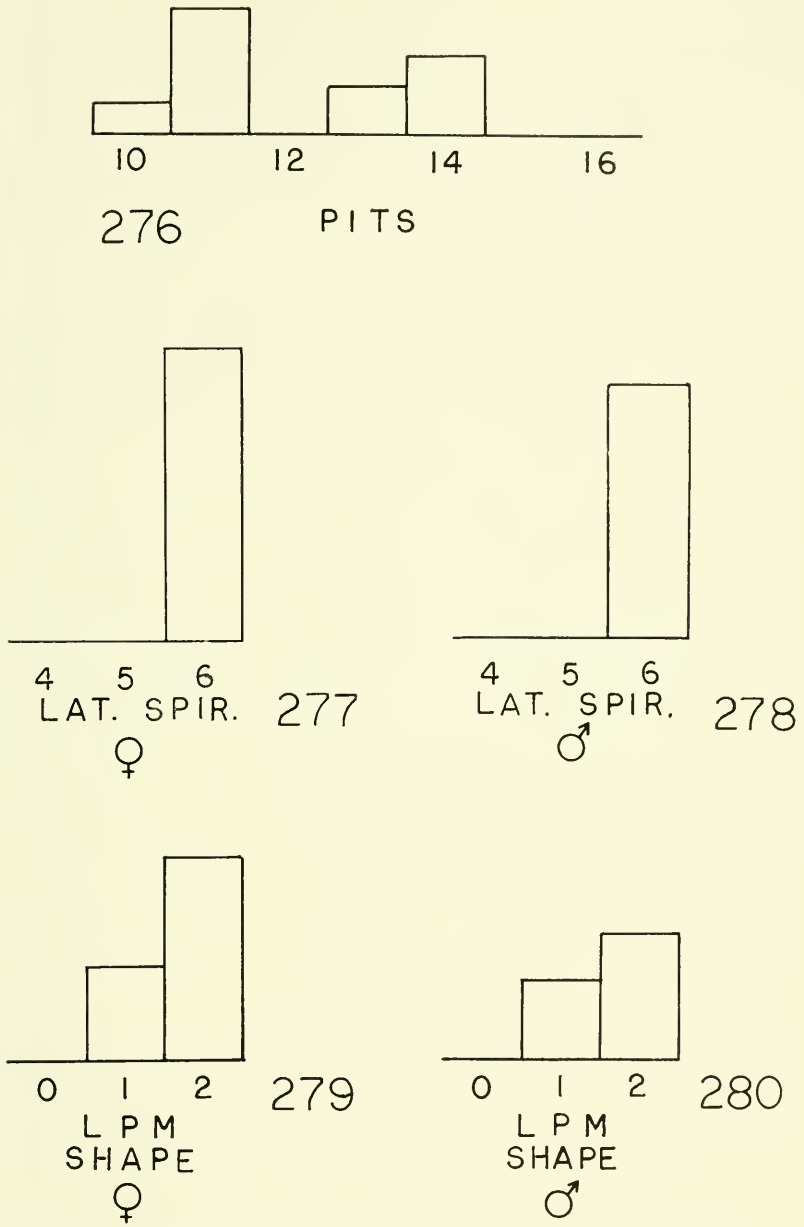
Using the above equation, several samples considered to be "pure" populations of each species were plotted (Figs. 260-261). These provided the reference material to judge suspected hybrid samples. Material from a number of suspected hybrid localities was then plotted so that their phenetic variation could be studied with reference to the pure samples (Figs. 262-275). The condition of the three discontinuous pupal characters and the male genitalia was noted for each hybrid swarm and, in the discriminant function graphs all samples except Park County #2, Wyoming (Fig. 275) had predominantly the discontinuous characters of *jamesi.* Some of the Park County #2 specimens had the male genitalia of *denningi,* while others had the *jamesi* genitalia. Often, however, a specimen had the discontinuous characters of both species. The *only* purpose of such notation is to prevent the backcrosses from being confused as non-hybrid individuals of one or the other species.

One characteristic of natural hybridization is animals, which is quite evident here, is the small number of hybrid individuals in the wild. This may be one reason for the paucity of records of natural hybrids in many groups of animals (see Stebbins, 1950). In several instances in this study, two or three reared specimens represented two hours' concentrated collecting.

Phenetically speaking, the most obvious example of hybridization between *jamesi* and *denningi* is found in material reared from a small stream in Custer County, Montana (Figs. 262-263). These graphs of specimens possessing the *jamesi* formula of spiracular openings on the respiratory horn and rounded *lpm* tubercles show a small number of specimens that fall almost exactly between the parental forms and a larger number which are phenetically virtually identical to *denningi* with respect to the seven characters employed. If we assume that dominance is lacking, then the intermediate cluster would represent F_1 progeny and the second, larger group on the left side of the graph are backcrosses between *denningi* and the F_1's.

Typical *Culicoides denningi* was not numerous at this locality at the time that this material was collected (2 ♀ ♀, 2 ♂ ♂).

One of the most striking modifications in the hybrids is the shape of the apex of the telomere. In *jamesi,* this structure is generally large with a bulbous, foot-shaped apex (Fig. 281); however, hybrids with *jamesi* genitalia have a slender apex, usually with only a slight swelling (Fig. 282). Good evidence for the multifactorial nature of the shape of the apex can be found in Figures 281 and 282. It is interesting that the shape of the apex of the telomere in the hybrids in some cases is almost identical to that found in *hieroglyphicus,* a species of more southern distribution. Figures 276 to 280 show the variation in number of sensory pits on both antennae, in lateral



Figs. **276-280.** Variation in naturally occurring hybrids between *C. (S.) jamesi* and *C. (S.) denningi* from Custer County, Montana. Sample sizes for females are 18 and for males 16. **276,** total number of antennal sensory pits in females ("pure" *denningi*=10, *jamesi*=14-16); **277-278,** total number of lateral spiracular openings on the pupal respiratory horn (*denningi*=4, *jamesi*=6); **279-280,** shape of *lpm* tubercles on the eighth abdominal segment, 0=spiniform, 1=semi-spiniform, 2=rounded (*denningi*=0, *jamesi*=2).

spiracular openings on the respiratory horn and in shape of *lpm* tubercles for the Custer County sample. The shape of the *lpm* tubercles in hybrid individuals is shown in Figures 283-284. The telomere from an individual with a predominantly *denningi* genitalia is shown in Figure 286 while the normal type of telomere is seen in Figure 285.

Hybrid swarms are generally found in disturbed or marginal habitats, particularly those which might be intermediate between the parental habitats and, therefore, to which neither parent is well adapted as the hybrids. The Custer County specimens were reared from a warm, stagnating stream which is not the usual environment of either *jamesi* or *denningi*. As indicated in the section of this paper dealing with biology of the immature stages, *jamesi* seems to have wider ecological tolerances than *denningi*. This apparently accounts for the greater abundance at this locality of individuals more closely resembling *jamesi* in such characters as *lpm* shape, spiracular openings on the horn, male genitalia, etc.

When hybridization occurs in a stable ecological situation, the breakdown of the well-adapted gene complexes of the parental forms should result in a number of ill-adapted combinations which generally will not survive. In marginal or unstable environments, however, there is a possibility that of the numerous hybrid segregates produced, a few might be able to stabilize and adapt themselves to the new environment. If the ecological conditions to which such a segregate is adapted persist, allowing the population to maintain itself, the result will be an extremely variable population, due to recombination of parental genomes, adapted to a new habitat. This is apparently the situation at the Custer County locality.

Graphs of the other samples show similar results. From Big Horn County, Montana (Figs. 266-267), four females which possess the *lpm* shape and spiracular formula of *jamesi* lie well within the phenetic limits of *denningi,* one female being placed slightly more toward *jamesi*. Of the two males with predominantly *jamesi* genitalia, one is more or less intermediate for the seven characters examined, the second more similar to *denningi*.

From Rosebud County, Montana, males with predominantly *jamesi* genitalia almost completely bridge the gap between *jamesi* and *denningi* (Fig. 264). Of the females with a *jamesi* respiratory horn pattern and *lpm* tubercles, one specimen is intermediate and the remaining five are identical to *denningi* with regard to the seven characters used (Fig. 265). Similar results were obtained for Elko County, Nevada (Figs. 273, 274). One female from Park County, Wyoming (#1) appears to be pure *jamesi* or a backcross between *jamesi* and an F_1, and another is very similar to *denningi* (Figs. 268-269). Of the remaining eight from this locality, three appear to be intermediate and five show variation toward *jamesi*. In the absence of dominance, this would imply gene flow from the hybrids toward *jamesi* parents by backcrossing.

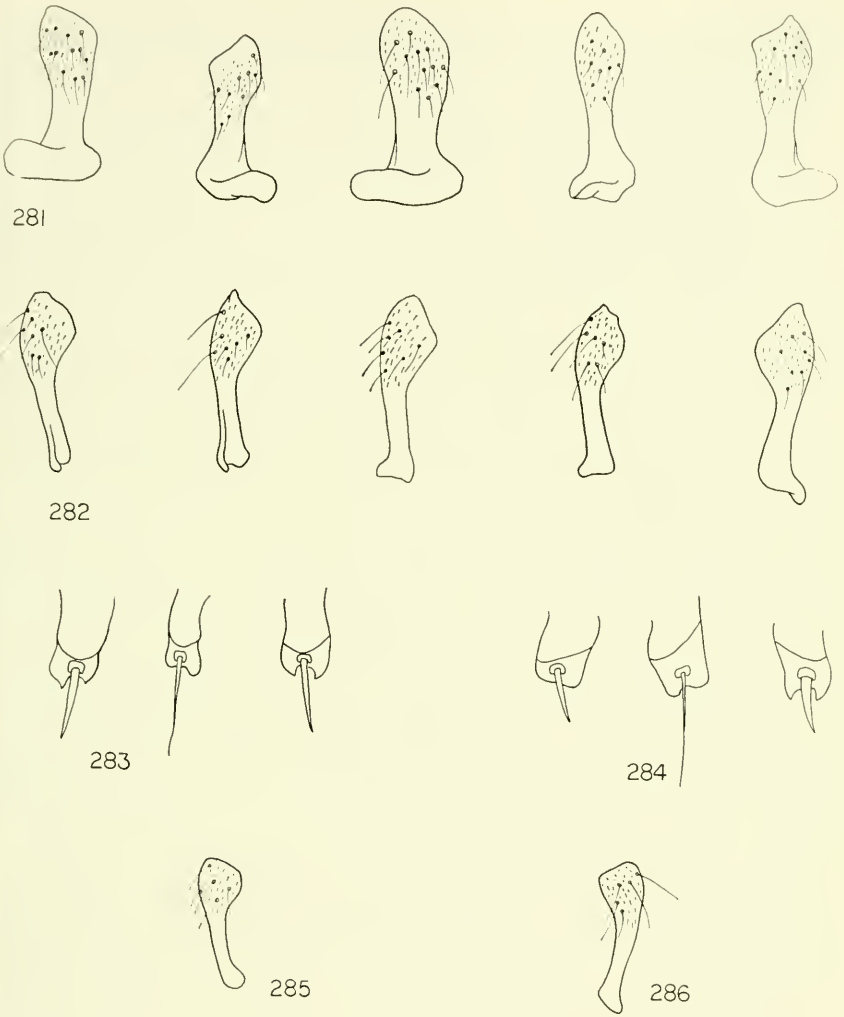


Fig. **281.** Telomeres of "pure" *C. (S.) jamesi.* Fig. **282.** Telomeres of hybrids between *C. (S.) jamesi* and *C. (S.) denningi.* All from individuals with predominantly *jamesi* genitalia. Fig. **283-284.** *lpm* tubercles of hybrids between *jamesi* and *denningi.* Fig. **285.** Telomere of "pure" *denningi.* Fig. **286.** Telomere of hybrid between *jamesi* and *denningi.* Taken from individual with predominantly *denningi* genitalia.

If some of these specimens are indeed results of backcrosses, we should carefully examine the populations proximate to the hybrid zone for examples of introgression. Introgression was described by Anderson and Hubricht (1938) as the infiltration of genetic material across an incompletely developed sterility barrier through backcrossing of F_1 hybrids to one or the other

parental forms, followed by selection of well adapted backcross types. This is usually taken to mean the spread of genes away from the area of hybridization into areas where one parental species occurs alone or where both occur hybridizing.

The detection of introgression involves the principle of correlation among characters. If two species are undergoing introgressive hybridization, the variation pattern of species A should be in the direction of species B in or near regions of sympatry. Introgressed individuals of species A should not possess random combinations of characters of species B, but rather each individual should vary in the direction of species B in several characteristics (Stebbins, 1950). The strength of phenotypic manifestation or expressivity, however, of a given block of introgressed genes will vary among individuals.

One must inject some caution here and point out that presence of a single variant character in individuals of a population does not necessarily indicate introgression but may result from mutation and selection for that character in a region where it is advantageous. This is particularly likely in cases of oligogenic characters.

Examination of flies from numerous localities away from the hybrid zone for cases of introgression revealed a number of specimens of *jamesi* from Sublette County, Wyoming, that closely resemble *denningi* in a number of characteristics (Figs. 271-272). Of the 13 female specimens examined, 10 had an antennal sensory formula of 3, 7-10 and the remaining three had 3, 5, 7-10. In addition, the third maxillary palpal segment was much longer than normally occurs in *jamesi,* and the width of the eye separation was quite large. All 20 males had three rather than the usual four antennal sensory pits and a narrower telomere apex. Further, several of the pupae of both sexes had spiniform or semi-spiniform *lasm* and semi-spiniform *lpm* tubercles. A large number of specimens were reared from this locality, and all but one were *jamesi.* The remaining specimen was a female of *denningi.*

The problem is to ascertain whether this lone specimen of *denningi* represents the remnant of a generation of that species that "peaked" before the collection was made and during that time hybridized with *jamesi,* resulting in the characteristics of the Sublette County sample. If this is so, the phenotypic variation of the specimens does not approach that of, for example, the Custer and Big Horn County samples. The females occur well toward the *denningi* on the hybrid graph, but the males appear only as members of a slightly more than usually variable population.

Although this population suggests introgression, final judgment must await closer scrutiny to see whether its attributes result from introgression or from hybridization between the *jamesi* population and *denningi.*

Hybridization between C. jamesi and C. hieroglyphicus

The females of *hieroglyphicus* and *jamesi* are even more similar than

those of *denningi* and *jamesi* and, consequently, are difficult to separate even by a discriminatory equation using pupal data. The use of principal components on a large number of pupal and adult characters indicates that hybridization occurs at two localities, Kane County, Utah, and San Miguel County, New Mexico. At both these localities as well as others, the two forms generally replace each other along an altitudinal gradient, *jamesi* occurring at higher elevations and *hieroglyphicus* at lower elevations. In the zone of overlap, hybridization occurs, as suggested by the results of a principal components analysis (Fig. 259). Three females, determined as *hieroglyphicus* by pupal characteristics, are apparently hybrids of that species and *jamesi*.

One of the greatest difficulties in analyzing possible hybridization between these two forms lies in distinguishing polarity of morphoclines from the effects of hybridization. The southern populations of *hieroglyphicus*, e.g., Brewster County, Texas, Chaves County, New Mexico, etc., have more abdominal segments with spiniform *lpm* tubercles than their northern counterparts, and two lateral spiracular openings on the respiratory horns, as opposed to three in many of the northern specimens. Since *jamesi* has rounded *lpm* tubercles and three lateral spiracular openings, one can easily see the difficulties encountered with separating the two taxa when they come together in Utah and northern New Mexico.

At present, nothing more definite can be said than that hybridization apparently occurs between these two forms in certain areas. Further elucidation will require extensive collecting in southern Utah and northern New Mexico, along altitudinal gradients, particularly where the two forms overlap.

Possible hybridization between C. denningi and C. hieroglyphicus

These two closely related species are basically allopatric, except for a rather narrow zone of overlap in northeastern Utah, northern Colorado and southern Wyoming. Collection of a large number of adults of *denningi* and *hieroglyphicus* at light in northeastern Utah revealed a number of possible intermediate specimens from Uintah and Grand counties. Some females thought to be *hieroglyphicus* on the basis of the short proboscis, third maxillary palpal segment, etc., had a wide interocular separation, antennal sensorial formula of 3, 7-10 and certain other attributes more indicative of *denningi*. More reared specimens and associated pupal skins are needed from these areas to determine if, in fact, hybridization is occurring.

The eastern and southern parts of Utah probably hold the key to understanding the relationships among *hieroglyphicus, denningi* and *jamesi*. All three species occur in this region, and in many instances two or all three occur together. I have seen numerous individuals from this area which

exhibit pupal and adult characters of all three species, suggesting three-way hybridization.

A critical analysis of associated larval, pupal and adult instars, utilizing the techniques of experimental taxonomy, may provide a solution to this problem, but an attempt to solve it on the basis of a morphological analysis of the adults alone will only more hopelessly confuse the situation.

Selfia and the subspecies concept

When one demonstrates hybridization between what are assumed to be "good" biological species, e.g., *C. jamesi* and *denningi,* or discusses geographic variation, he must deal with the antiquated subspecies concept. I find little to be gained from formal infraspecific names. In addition to placing an unnecessary burden on formal nomenclature, naming of subspecies emphasizes differences that may be artificial; more importantly, it fails in its primary purpose of providing an adequate description of the variation.

Often the decision to name a subspecies has been subjective evaluation based on only a few characters with little knowledge of patterns of geographic variation throughout the range of the animal. When a number of characters are examined by statistical techniques, the shallowness of this endeavor is even more evident since as the number of characters is increased, so is the number of possible infraspecific groups. Even when numerous samples of a particular organism are analyzed by multivariate statistical means, the results are often rather ambiguous and subject to different interpretations. A good example is the *Culicoides variipennis* situation, as outlined by Wirth and Jones (1957) but criticized by Atchley (1967). Fortunately, with a few exceptions, the taxonomy of *Culicoides* has not been plagued with subspecific names.

With these points in mind, variation has been described above for three species of *Selfia* and summarized in three-dimensional models. Distinct clusters of populations were pointed out and the trends in variation demonstrated, but subspecies were not named for a very practical reason. I have repeatedly pointed out in this paper that females of *denningi, hieroglyphicus* and *jamesi* are not separable without resorting to the immature stages. Consequently, very little is to be gained by describing clusters of populations as subspecies if, because of the great morphological similarity of the adults, you cannot determine to which species the subspecies belong.

Evidence of hybridization between populations if often taken to mean conspecificity. The production of F_1 progeny as a result of interbreeding implies only that a pre-mating isolating mechanism, or genic or chromosomal sterility has broken down, if, in fact, they ever existed. Without experimental studies or support from cytogenetics, little evidence can be marshalled as to indicate whether the F_1 offspring are sterile, since there is

often little correlation between reproductive isolation and visible morphological differences. Even if the F_1 progeny are fertile, the breakdown of adaptive gene combinations and disharmonious interactions between parental genes in the hybrid segregates may insure that the two species are, in fact, separated by an isolating mechanism.

The production of F_1 or F_2 progeny and backcrosses by interbreeding between *jamesi* and *denningi* is *not* necessarily evidence of conspecificity and, accordingly, I have referred to them as species.

Cladistic evidence supports this stand, since not only are *denningi* and *jamesi* members of separate species groups, the former is apparently the more primitive species of the *hieroglyphicus* group, while *jamesi* is the more specialized member of the *jacksoni* group.

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TABLE 1. Summary of pupal characters of *Culicoides (S.) multipunctatus.*

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	203	±7.6	189-205	9
	M	181	±6.9	172-189	7
am spine length	F	35	±3.2	31-39	7
	M	35	±2.6	31-38	7
ad spine length	F	27	±2.3	25-32	9
	M	26	±2.4	22-30	7
d_1 spine length	F	21	±2.2	18-26	9
	M	19	±1.9	16-22	7
d_2 spine length	F	18	±3.3	13-23	9
	M	16	±2.1	13-18	7
d_3 spine length	F	6	±0.2	5-6	9
	M	6	±0.4	5-6	7
Operculum length	F	198	±8.8	183-205	6
	M	180	±7.7	174-192	7
Operculum width	F	148	±7.1	136-155	7
	M	130	±6.1	123-140	7
Operculum width/*am* spine	F	4.3		3.90-5.0	7
	M	3.8		3.24-4.06	7
Total number apical spiracle openings	F	9		8-10	9
	M	8		7-8	7
d_3/d_1	F	0.28		0.25-0.33	9
	M	0.30		0.25-0.37	6
d_3/d_2	F	0.33		0.26-0.46	9
	M	0.36		0.29-0.46	6

TABLE 2. Summary of pupal characters of *Culicoides (S.) brookmani* Wirth.

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	220	±10.4	202-234	8
	M	213	±11.0	202-232	6
am spine length	F	62	± 4.2	56-68	10
	M	59	± 5.6	48-67	8
ad spine length	F	56	± 3.5	52-62	10
	M	51	± 3.9	46-58	8
d_1 spine length	F	42	± 2.8	39-46	10
	M	37	± 3.3	32-43	8
d_2 spine length	F	35	± 2.6	32-40	10
	M	31	± 2.2	27-35	8
d_3 spine length	F	9	± 2.6	5-12	10
	M	9	± 0.3	8-10	8
Operculum length	F	170	± 5.9	164-180	10
	M	178	± 4.7	170-186	8
Operculum width	F	153	± 5.4	146-161	10
	M	143	± 6.6	130-149	8
Operculum width/*am* spine	F	2.5		2.28-2.77	10
	M	2.5		2.19-2.98	8
d_3/d_1	F	0.22		0.11-0.36	10
	M	0.25		0.21-0.28	8
d_3/d_2	F	0.26		0.14-0.39	10
	M	0.29		0.26-0.33	8

Table 3. Summary of pupal characters of *Culicoides (S.) denningi.*

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	170	± 5.3	158-178	8
	M	173	±12.8	155-184	5
am spine length	F	31	± 2.3	25-32	8
	M	29	± 3.5	26-35	5
ad spine length	F	23	± 2.0	20-26	8
	M	23	± 2.2	21-26	5
d_1 spine length	F	17	± 2.4	13-21	8
	M	17	± 1.6	16-20	5
d_2 spine length	F	13	± 2.7	10-17	8
	M	15	± 1.9	13-17	5
d_3 spine length	F	5	± 1.3	4-6	8
	M	5	± 0.0	0	5
Operculum length	F	190	± 9.2	186-205	8
	M	190	±10.0	177-202	5
Operculum width	F	155	± 2.6	152-161	8
	M	138	± 8.3	130-152	5
Operculum width/*am* spine	F	5.1		4.84-6.20	8
	M	4.7		4.33-5.50	5
Total number apical spiracle openings	F	11.5		11-14	8
	M	12.6		10-14	5

Table 4. Localities and sample sizes of the specimens of *C. denningi* measured.

Locality	N ♂	N ♀
1. UTAH, Garfield Co., Sevier R.	4	3
2. UTAH, Garfield Co., E. Fork Siever R., 3 mi. W. Ruby's Inn	3	3
3. UTAH, Juab Co., Sevier R., 20 mi. S. W. Nephi	8	8
4. UTAH, Millard Co., Delta (north edge)	5	2
5. UTAH, Unitah Co., Green R., Dinosaur Nat'l Mont.	14	14
6. NEVADA, Elko Co., Salmon Falls Ck., 2 mi. S. Jackpot	1	5
7. NEVADA, Elko Co., N. Fork Humbolt R., 16 mi. N. E. Elko	4	8
8. NEVADA, Elko Co., Hendricks Ck., S. E. Mountain City	1	
9. WYOMING, Sublette Co., Cottonwood Ck., 10 mi. S. Daniel*		
10. WYOMING, Converse Co., Boxelder Ck., S. E. Glenrock	1	
11. WYOMING, Park Co., Cottonwood Ck., N. Cody		6
12. WYOMING, Park Co., Big Sand Coulee, 13 mi. S. Belfry	6	
13. WYOMING, Fremont Co., Poison Water Ck., 1 mi. S. W. Shoshoni		2
14. MONTANA, Custer Co., Pumpkin Ck., 30 mi. N. Volborg	2	
15. MONTANA, Big Horn Co., 12 mi. S. Custer		5
16. SASKATCHEWAN, S. Saskatchewan R., Saskatoon	10	9

* Not included in discriminant function analysis.

TABLE 5. Means of 10 localities (see Table 4) and 16 characters for females of *C. denningi*. Values for characters 1-3 are in mm; 4-6, 8-10 and 12-16 are in microns. For explanation of character codes, see section on statistical methods.

Character	Locality									
	1	2	3	4	5	6	7	11	13	15
1	1.43	1.32	0.98	1.06	1.13	1.13	0.98	1.34	1.24	1.05
2	0.66	0.62	0.46	0.50	0.53	0.54	0.45	0.62	0.58	0.49
3	0.82	0.74	0.54	0.58	0.63	0.63	0.54	0.75	0.66	0.58
4	561	533	408	457	460	477	392	550	522	451
5	290	270	209	234	236	246	200	277	268	231
6	271	264	200	223	224	231	193	262	254	221
7	9.33	10.00	10.00	10.00	9.93	9.80	10.12	10.00	10.00	10.40
8	424	406	310	329	361	366	300	402	392	341
9	217	219	167	174	189	190	160	211	202	179
10	207	194	143	158	172	177	140	191	191	162
11	35.33	34.00	29.75	29.00	31.00	31.00	26.37	35.66	31.00	28.40
12	101	92	68	78	79	86	68	94	93	73
13	39	34	29	28	30	31	30	34	37	29
14	495	454	332	381	388	400	332	470	459	366
15	493	460	330	375	384	395	328	471	452	364
16	260	243	179	197	205	206	172	255	246	197

Table 6. Means of 11 localities (see Table 4) and 10 characters for males of *C. denningi*. Values for characters 1-3 are in mm; 5-10 are in microns.

Character	Locality 1	2	3	4	5	6	7	8	10	11	14
1	1.16	1.14	0.87	0.94	0.99	0.97	0.88	1.03	1.13	1.15	1.01
2	0.46	0.45	0.35	0.38	0.40	0.41	0.36	0.41	0.46	0.46	0.41
3	0.57	0.57	0.41	0.46	0.48	0.49	0.42	0.49	0.54	0.57	0.49
4	6.00	6.00	6.00	6.00	6.00	6.00	6.00	6.00	6.00	6.16	6.00
5	64	63	51	53	55	56	48	59	68	63	56
6	434	429	322	356	365	366	327	369	403	436	384
7	432	424	327	351	369	372	322	378	412	433	387
8	222	225	170	183	191	195	168	192	229	232	205
9	88	91	76	82	84	84	74	87	90	89	88
10	12	12	10	10	10	9	11	9	9	14	14

TABLE 7. Pooled within locality variance-covariance matrix for 16 adult female characters of *C. denningi*. Values have been multiplied by 10^5, thus "26878"=.26878. The variances are found along the diagonal, the covariances comprise the remainder of the matrix. The character codes refer to those given in the text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	26878															
2	12020	8872														
3	15869	7758	12265													
4	7274	3924	4901	4067												
5	4856	2777	3170	2185	1534											
6	3282	1506	2259	1568	808	893										
7	−1562	−701	−1119	−505	−192	−310	12200									
8	4831	2913	3500	1694	1145	797	−744	1959								
9	2435	1370	1756	967	589	420	−570	1103	780							
10	2353	1474	1710	681	524	363	−226	821	310	500						
11	20676	7528	13899	10509	7040	5419	−1000	7759	3013	5124	558700					
12	1585	976	1069	406	313	250	−329	424	167	243	3708	297				
13	535	264	349	140	97	79	−202	141	80	57	849	58	37			
14	7705	3708	5080	2288	1516	1008	−617	1539	715	792	8655	603	190	3540		
15	8981	4374	5790	2708	1717	1232	−403	1841	899	904	12493	659	193	3971	4970	
16	5281	2845	13670	1786	1167	770	−462	1133	580	525	5716	363	125	1993	2364	1518

Table 8. Pooled within locality variance-covariance matrix for 10 adult male characters of *C. denningi*. Values have been multiplied by 10^5, thus "17330," thus .17330. The variances are found along the diagonal, the covariances comprise the remainder of the matrix. The character codes refer to those given in the text.

	1	2	3	4	5	6	7	8	9	10
1.	17330									
2.	4658	2676								
3.	7129	2035	5110							
4.	−1082	−430	750	2200						
5.	676	161	240	−28	136					
6.	4337	1276	2181	96	274	2140				
7.	4225	1114	2394	−313	247	1914	2301			
8.	2566	773	1363	0	153	988	1038	863		
9.	2062	219	308	108	11	253	227	162	152	
10.	66	−20	120	28	−14	23	30	25	−1	32

Table 9. Summary of pupal characters of *Culicoides (S.) hieroglyphicus*.

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	220	±8.4	208-236	15
	M	215	±8.0	202-226	13
am spine length	F	41	±3.7	32-46	15
	M	36	±2.6	32-42	13
ad spine length	F	32	±2.8	27-36	15
	M	31	±2.0	26-36	13
d_1 spine length	F	25	±2.6	21-29	15
	M	24	±2.0	22-29	13
d_2 spine length	F	17	±2.6	13-23	15
	M	17	±2.6	13-22	13
d_3 spine length	F	6	±1.6	4-9	15
	M	6	±1.8	4-9	13
Operculum length	F	202	±5.9	195-220	15
	M	203	±7.5	195-217	13
Operculum width	F	164	±5.9	149-170	15
	M	146	±5.7	136-155	13
Operculum width/*am* spine	F	4.0		3.35-4.32	15
	M	4.1		3.48-4.56	13
Total number apical spiracle openings	F	15		14-16	15
	M	14		12-16	13

TABLE 10. Localities and sample sizes of the specimens of *C. (S.) hieroglyphicus* measured.

Locality	N ♂	♀
1. TEXAS, Brewster Co.	10	9
2. NEW MEXICO, Chaves Co., Pecos R., 7 mi. E. Roswell	12	15
3. NEW MEXICO, San Miguel Co., Tecolote Ck., Tecolote	21	11
4. ARIZONA, Pima Co.*	1	1
5. ARIZONA, Yavapai Co., Red Rock Crossing	2	2
6. CALIFORNIA, Kern Co.	10	5
7. UTAH, Kane Co., E. Fork Virgin R., Mt. Carmel Jct.	11	9
8. UTAH, Garfield Co., Escalante R., 15 mi. E. Escalante	4	8
9. UTAH, Wayne Co., Fremont R., Hanksville	3	
10. UTAH, Wayne Co., Fremont R., 15 mi. W. Hanksville	4	
11. UTAH, Wayne Co., Fremont R., Capitol Reef Nat'l. Mont.	10	8
12. UTAH, San Juan Co., San Juan R., 2 mi. E. Bluff	12	11
13. UTAH, Grand Co., 1 mi. S. W. Cisco	11	15
14. UTAH, Carbon Co., Coal Ck., 2 mi. E. Wellington	2	5
15. KANSAS, Meade Co., 3 mi. E. Meade State Lake	2	

* Not included in discriminant function analysis.

Table 11. Means of 11 localities (see Table 10) and 16 characters for females of *C. hieroglyphicus*. Values for characters 1-3 are in mm; 4-6, 8-10 and 12-16 are in microns. For explanation of character codes, see section on statistical methods.

	Locality										
Character	1	2	3	5	6	7	8	11	12	13	14
1	0.95	1.14	1.29	1.00	1.09	1.18	1.13	1.11	1.08	0.99	1.17
2	0.46	0.55	0.60	0.46	0.54	0.56	0.53	0.53	0.52	0.47	0.56
3	0.51	0.63	0.72	0.55	0.61	0.66	0.63	0.62	0.60	0.54	0.65
4	427	480	503	429	458	496	477	468	474	432	494
5	210	247	266	214	229	252	241	239	242	218	248
6	217	239	254	215	229	244	235	228	232	213	245
7	13.33	14.20	10.91	13.50	10.00	11.55	10.62	10.50	10.54	10.13	13.20
8	316	365	366	318	332	357	337	335	332	317	347
9	178	190	202	178	186	195	186	188	182	176	185
10	138	160	165	140	146	161	151	146	150	140	162
11	29.00	30.93	32.00	31.00	31.00	32.11	29.50	31.12	31.45	29.60	30.00
12	65	78	80	70	72	75	70	68	70	64	78
13	32	37	36	31	33	35	32	33	33	33	38
14	356	417	455	367	394	433	411	398	389	354	418
15	341	406	448	355	389	423	402	392	387	343	412
16	188	224	249	194	210	228	224	215	215	188	221

TABLE 12. Means of 14 localities (see Table 10) and 10 characters for males of *C. hieroglyphicus*. Values for characters 1-3 are in mm; 5-10 are in microns. For explanation of character codes, see section on statistical methods.

Character	Locality 1	2	3	5	6	7	8	9	10	11	12	13	14	15
1	0.84	0.94	1.04	0.98	0.95	1.00	0.96	0.93	0.89	0.97	0.93	0.85	1.00	0.87
2	0.34	0.40	0.43	0.39	0.39	0.41	0.40	0.39	0.38	0.40	0.39	0.36	0.41	0.36
3	0.39	0.45	0.51	0.47	0.46	0.47	0.46	0.44	0.42	0.46	0.45	0.40	0.47	0.41
4	7.00	6.92	6.28	6.00	6.10	6.18	6.00	6.00	6.00	6.00	6.17	6.09	7.00	8.00
5	50	55	60	53	53	56	52	53	50	53	53	46	56	51
6	340	377	401	367	367	386	367	357	342	366	361	324	377	338
7	328	366	392	367	361	378	361	350	331	361	356	316	375	330
8	174	194	216	198	190	207	205	191	186	196	197	170	209	170
9	85	91	93	88	85	92	88	89	87	87	89	86	90	88
10	17	19	22	19	17	23	20	24	19	19	22	21	26	20

Table 13. Pooled within locality variance-covariance matrix for 16 adult female characters of *C. hieroglyphicus*. Values have been multiplied by 10^5, thus "18943"=.18943. The variances are found along the diagonal, the covariances comprise the remainder of the matrix. The character codes refer to those given in the text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	18943															
2	6363	3707														
3	11394	3705	9286													
4	3623	1895	1656	5278												
5	3520	867	1539	1101	934											
6	3448	866	1466	753	358	660										
7	−7331	−676	−1808	2970	1147	−335	150800									
8	4994	2214	3304	1891	932	852	−4386	7665								
9	2283	1022	1447	631	365	306	−1767	1239	753							
10	1399	568	872	489	300	285	468	804	251	433						
11	24563	11045	16039	6017	2768	1181	2000	397	6402	1345	569000					
12	1016	376	713	301	160	169	304	364	145	149	1767	209				
13	244	68	217	121	41	246	177	183	77	15	1643	45	86			
14	5404	1937	3508	1221	1031	828	3119	1290	739	614	6085	315	56	2648		
15	5714	1832	3897	994	996	860	118	1656	739	607	3751	370	79	2421	2768	
16	3422	1199	2251	768	507	531	12	1220	475	414	5199	211	33	1314	1353	1183

TABLE 14. Pooled within locality variance-covariance matrix for 10 adult male characters of *C. hieroglyphicus*. Values have been multiplied by 10^5, thus "27231"=.27231. The variances are found along the diagonal, the covariances comprise the remainder of the matrix. The character codes refer to those given in the text.

	1	2	3	4	5	6	7	8	9	10
1.	27231									
2.	8622	5283								
3.	12944	4298	8533							
4.	−9004	−2952	−4317	44300						
5.	1089	382	574	40	154					
6.	7180	2363	3842	−2843	332	3232				
7.	7781	2310	4303	−3546	397	3100	3800			
8.	4823	1549	2467	−1764	239	1804	1910	1401		
9.	812	288	395	−294	35	312	319	179	108	
10.	511	167	239	−512	17	164	189	135	17	149

TABLE 15. Summary of pupal characters of *Culicoides (S.) jacksoni*.

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	220	±15.0	180-240	14
	M	210	± 5.7	203-220	7
am spine length	F	46	± 3.6	37-51	14
	M	43	± 1.0	41-47	7
ad spine length	F	39	± 3.5	35-42	14
	M	35	± 2.4	30-36	7
d_1 spine length	F	28	± 3.0	23-31	14
	M	27	± 2.9	18-26	7
d_2 spine length	F	21	± 5.0	18-23	14
	M	21	± 2.8	18-26	7
d_3 spine length	F	12	± 2.0	9-16	14
	M	14	± 2.5	9-16	7
Operculum length	F	197	±13.7	160-210	14
	M	199	±10.8	180 210	7
Operculum width	F	159	± 7.5	140-170	14
	M	149	± 7.1	140-160	7
Operculum width/*am* spine	F	4.1		3.68-5.0	14
	M	3.4		3.19-3.70	7
Total number apical spiracle openings	F	14.43		12-17	14
	M	14.43		14-16	7

Table 16. Summary of pupal characters of *Culicoides (S.) tenuistylus.*

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	194	± 9.8	181-206	5
	M	187	±11.4	183-202	4
am spine length	F	36	± 2.4	34-39	4
	M	35	± 8.6	27-46	4
ad spine length	F	28	± 1.6	27-30	5
	M	29	± 6.5	23-38	4
d_1 spine length	F	21	± 0.8	20-22	5
	M	23	± 2.2	21-26	4
d_2 spine length	F	19	± 1.3	17-20	5
	M	19	± 2.2	17-22	4
d_3 spine length	F	10	± 1.4	9-12	4
	M	11	± 2.0	10-12	4
Operculum length	F	189	± 0.0	0	3
	M	191	± 6.4	186-191	3
Operculum width	F	148	± 6.2	143-155	3
	M	139	± 0.0	0	3
Operculum width/*am* spine	F	4.0		3.74-4.20	3
	M	3.6		3.02-4.09	2
Total number apical spiracle openings	F	14		13-16	4
	M	13		11-16	4
d_3/d_1	F	0.49		0.47-0.53	3
	M	0.49		0.45-0.53	5
d_3/d_2	F	0.55		0.50-0.60	3
	M	0.58		0.53-0.64	4
d_1-d_2 distance/d_2-d_3	F	0.84		0.72.1.0	4
	M	0.79		0.71-0.82	4

TABLE 17. Summary of pupal characters of *Culicoides (S.) jamesi*.

Character	Sex	Mean length (μ) or ratio	SD	Range	N
Respiratory horn	F	219	±10.5	205-239	18
	M	216	±12.3	200-225	16
am spine length	F	42	± 3.6	34-48	18
	M	41	± 3.3	36-46	16
ad spine length	F	33	± 3.2	27-36	18
	M	32	± 3.9	26-43	16
d_1 spine length	F	26	± 3.0	22-30	18
	M	27	± 3.1	22-31	16
d_2 spine length	F	21	± 4.1	16-23	18
	M	19	± 3.3	13-23	16
d_3 spine length	F	9	± 1.1	8-13	18
	M	9	± 3.1	6-16	16
Operculum length	F	207	±11.0	189-226	18
	M	209	±12.6	195-236	16
Operculum width	F	167	± 8.5	152-180	18
	M	150	± 7.9	136-161	16
Operculum width/*am* spine	F	3.96		3.37-4.82	18
	M	3.69		3.44-4.30	16
Total number apical spiracle openings	F	13.4		10-17	18
	M	12.4		10-17	16
d_3/d_1	F	0.38		0.28-0.59	18
	M	0.37		0.26-0.59	16
d_3/d_2	F	0.51		0.36-0.81	18
	M	0.52		0.38-0.73	16
d_1-d_2 distance/d_2-d_3	F	0.69		0.45-0.97	18
	M	0.75		0.57-1.0	13

Table 18. Localities and sample sizes of the specimens of *C. jamesi* measured.

Locality	N ♂	♀
1. NEW MEXICO, San Miguel Co., Tecolote Ck., Tecolote	6	3
2. COLORADO, Jefferson Co., Soda Ck.	4	2
3. CALIFORNIA, San Luis Obispo Co.	5	5
4. UTAH, Kane Co., E. Fork Virgin R., Mt. Carmel Jct.	7	8
5. UTAH, Garfield Co., Paria R., N. Henrieville	1	5
6. UTAH, Garfield Co., Upper Valley Ck., 5 mi. E. Escalante	3	1
7. UTAH, Garfield Co., Pine Ck., 8 mi. N. Escalante	3	4
8. UTAH, Garfield Co., Escalante R., 15 mi. W. Escalante	2	5
9. UTAH, Wayne Co., Fremont R., Capitol Reef Nat'l Mont.	2	2
10. UTAH, Wayne Co., 2 mi. N. E. Bicknell	3	4
11. UTAH, Duchesne Co., Willow Ck., 12 mi. N. Castle Gate	11	14
12. UTAH, Uintah Co., Green R., Dinosaur Nat'l. Mont.	4	3
13. UTAH, Morgan Co., 16 mi. S. Wasatch	1	4
14. WYOMING, Converse Co., Boxelder Ck., S. E. Glenrock	6	4
15. WYOMING, Natrona Co., Bates Ck., S. Casper	5	8
16. WYOMING, Fremont Co., Poison Water Ck., 1 mi. S. W. Shoshoni		1
17. WYOMING, Platte Co., 20 mi. N. W. Wheatland	2	8
18. WYOMING, Sublette Co., Cottonwood Ck., 10 mi. S. Daniel	11	12
19. WYOMING, Park Co., Cottonwood Ck., N. Cody	5	10
20. WYOMING, Park Co., Big Sand Coulee, 13 mi. S. Belfry	2	1
21. WYOMING, Weston Co., Stockade Beaver Ck., 10 mi. N. Newcastle	8	6
22. MONTANA, Big Horn Co., 12 mi. S. Custer	3	7
23. MONTANA, Custer Co., Pumpkin Ck., 30 mi. N. Volborg	13	19
24. MONTANA, Rosebud Co., 6 mi. W. Forsyth	10	6
25. NEVADA, Elko Co., Hendricks Ck., S. E. Mountain City	8	6
26. UTAH, Garfield Co., E. Fork Sevier R., 3 mi. W. Ruby's Inn	3	6

TABLE 19. Means of 25 localities (see Table 18) and 16 characters for females of *C. jamesi*. Values for characters 1-3 are in mm; 4-6, 8-10 and 12-16 are in microns. For explanation of character codes, see section on statistical methods.

	Locality												
Character	1	2	3	4	5	6	7	8	9	10	11	12	13
1	1.28	1.32	1.01	1.19	1.01	1.04	0.98	1.09	1.10	1.14	1.27	1.18	1.25
2	0.55	0.60	0.50	0.57	0.49	0.49	0.46	0.53	0.52	0.54	0.60	0.56	0.58
3	0.73	0.74	0.56	0.68	0.55	0.55	0.53	0.61	0.61	0.64	0.70	0.64	0.70
4	505	556	446	505	446	450	418	464	471	480	511	478	515
5	253	274	224	255	226	226	209	236	239	237	265	242	259
6	252	282	222	250	221	223	209	228	232	242	249	237	256
7	15.00	15.00	13.40	14.62	12.40	14.00	14.25	12.80	14.00	13.75	14.28	10.66	12.50
8	347	380	307	372	323	326	317	340	347	339	376	360	373
9	189	206	173	205	179	177	181	185	192	184	204	194	203
10	158	174	134	167	144	149	138	154	155	156	171	165	170
11	30.66	30.00	28.60	34.12	29.60	30.00	27.25	28.60	31.50	33.00	33.64	33.33	32.00
12	75	77	60	77	64	71	57	70	74	69	80	78	78
13	31	32	30	35	30	34	29	31	31	31	34	32	34
14	432	479	365	439	367	378	348	379	397	402	440	403	450
15	428	462	353	430	357	356	332	376	409	396	432	403	450
16	237	250	192	234	193	198	177	201	214	215	235	214	228

Table 19. (Continued.)

Character	Locality 14	15	16	17	18	19	20	21	22	23	24	25
1	1.34	1.17	1.27	1.22	1.24	1.24	1.32	1.19	1.02	1.16	1.08	1.14
2	0.63	0.55	0.60	0.58	0.59	0.58	0.60	0.56	0.48	0.55	0.53	0.54
3	0.76	0.64	0.71	0.68	0.68	0.69	0.77	0.69	0.56	0.67	0.60	0.62
4	541	468	521	507	488	504	549	493	448	496	479	484
5	267	235	257	254	250	258	279	251	227	255	243	246
6	274	233	264	253	238	246	270	243	220	241	237	238
7	15.50	14.62	15.00	15.62	10.50	12.30	10.00	13.66	11.71	12.10	11.33	11.16
8	376	352	378	367	385	373	418	364	338	376	357	378
9	205	192	195	196	196	200	217	192	178	199	190	197
10	170	160	183	171	188	173	202	172	160	178	167	181
11	35.25	32.50	31.00	31.50	36.33	33.20	37.00	31.50	27.86	31.74	31.50	32.83
12	87	74	90	81	89	82	96	81	73	80	76	86
13	33	32	37	35	33	32	34	32	29	31	31	32
14	466	406	465	441	423	434	471	429	356	410	393	400
15	456	399	443	426	425	431	471	423	355	403	393	398
16	256	216	245	229	222	228	257	227	188	220	208	210

TABLE 20. Means of 25 localities (see Table 18) and 10 characters for males of *C. jamesi*. Values for characters 1-3 are in mm; 5-10 are in microns. For explanation of character codes, see section on statistical methods.

Character	Locality 1	2	3	4	5	6	7	8	9	10	11	12	13
1	1.12	1.26	0.99	1.04	0.92	0.95	0.84	0.97	1.07	1.02	1.08	1.06	1.07
2	0.46	0.50	0.39	0.41	0.36	0.39	0.34	0.38	0.43	0.41	0.43	0.43	0.44
3	0.56	0.63	0.47	0.52	0.44	0.45	0.42	0.47	0.52	0.50	0.53	0.53	0.50
4	8.83	10.25	7.40	7.42	5.00	7.33	7.00	8.00	7.00	7.67	8.00	7.00	7.00
5	57	64	51	56	50	52	41	50	59	51	57	54	56
6	414	491	356	402	351	356	308	361	398	377	404	381	418
7	408	483	353	396	372	354	312	361	398	381	402	378	418
8	219	244	188	209	189	189	164	191	211	198	210	199	211
9	113	119	102	109	108	106	94	104	113	104	113	108	118
10	44	52	46	52	46	46	44	51	39	52	47	38	43

TABLE 20. (Continued.)

Character	Locality 14	15	17	18	19	20	21	22	23	24	25	26
1	1.16	0.99	1.11	1.13	1.10	1.13	1.03	0.91	1.06	0.98	1.02	1.12
2	0.46	0.40	0.46	0.46	0.44	0.46	0.42	0.39	0.44	0.40	0.41	0.45
3	0.58	0.48	0.57	0.54	0.54	0.58	0.51	0.44	0.54	0.48	0.49	0.56
4	9.00	7.40	10.00	5.91	6.40	7.50	7.75	8.33	6.53	6.40	6.12	8.00
5	60	51	57	59	59	59	58	52	61	55	57	56
6	435	364	411	411	409	431	399	355	399	374	378	411
7	439	360	406	411	407	428	400	350	391	368	379	417
8	222	188	200	210	213	229	208	177	209	192	197	211
9	120	105	108	113	112	115	111	101	108	107	108	117
10	49	38	51	36	33	26	38	21	19	33	31	45

Table 21. Pooled within locality variance-covariance matrix for 16 adult female characters of *C. jamesi*. Values have been multiplied by 10^5, thus "31149"=.31149. The variances are found along the diagonal, the covariances comprise the remainder of the matrix. The character codes refer to those given in the text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	31149															
2	13133	8508														
3	17192	7587	13935													
4	7356	3540	4308	3090												
5	3499	1725	1965	1648	1117											
6	3802	1784	2324	1405	549	876										
7	16322	6740	6753	3937	149	4005	203000									
8	4454	2377	2636	1513	811	726	4046	1629								
9	2242	1142	1272	742	403	345	2288	868	622							
10	2172	1219	1344	754	400	372	1693	753	245	504						
11	28056	15350	13530	9486	3602	5816	6800	5400	1845	3494	518400					
12	1798	967	1087	568	277	308	1147	443	202	240	3240	291				
13	300	126	210	149	74	82	484	70	49	651	660	48	46			
14	9838	4808	5622	2939	1390	1486	6318	1809	810	984	15723	678	117	4482		
15	9197	4492	5108	2731	1384	1314	7424	1783	829	943	12645	664	93	4032	4539	
16	4372	2153	2515	1377	691	674	2569	805	385	411	5658	337	58	1816	1928	1238

TABLE 22. Pooled within locality variance-covariance matrix for 10 adult male characters of *C. jamesi*. Values have been multiplied by 10^5, thus "18232"= .18232. The variances are found along the diagonal, the covariances comprise the remainder of the matrix. The character codes refer to those given in the text.

	1	2	3	4	5	6	7	8	9	10
1.	18232									
2.	4996	3230								
3.	9126	2722	6658							
4.	3050	1796	4539	93500						
5.	971	238	432	260	142					
6.	5684	1736	2582	1652	340	3228				
7.	6456	1943	3209	2384	384	3246	4127			
8.	3256	992	1421	654	188	1545	1716	1284		
9.	1053	282	471	344	59	485	505	241	168	
10.	264	95	–22	595	–5	215	258	68	33	325

Table 23. List of characters employed in principal components study. Characters with asterisk were used in generalized discriminant functions.

Character code number	Character	Sex or life history stage
1.*	Lenth of wing from basal arculus to tip	♀ ♂
2.*	Width of wing at broadest point	♀ ♂
3.*	Length of costa	♀ ♂
4.*	Length of flagellum	♀
5.*	Length of distal 5 flagellomeres	♀
6.*	Length of proximal 8 flagellomeres	♀
7.	Length of antennomere 11	♀
8.	Length of antennomeres 9+10	♀
9.*	Number of antennal sensory pits (sum of both antennae)	♀ ♂
10.*	Length of head and proboscis combined	♀
11.*	Length of head from interocular seta to tormae	♀
12.*	Length of proboscis from tormae to tip of labrum	♀
13.	Width of eye separation	♀
14.*	Number of maxillary teeth (sum of both maxillae)	♀
15.	Length of 2nd segment of maxillary palp	♀ ♂
16.*	Length of 3rd segment of maxillary palp	♀ ♂
17.	Length of 4th segment of maxillary palp	♀ ♂
18.	Length of 5th segment of maxillary palp	♀ ♂
19.*	Width of 3rd segment of maxillary palp	♀
20.	Number of multiple antennal sensory pits on other than 3 (sum of both antennae)	♀ ♂
21.*	Length of femur	♀ ♂
22.*	Length of tibia	♀ ♂
23.*	Length of basitarsus	♀ ♂
24.	Length of 2nd tarsomere	♀ ♂
25.	Number of tibial spines on hind leg (sum of both legs)	♀ ♂
26.*	Length of telomere	♂
27.*	Width of telomere tip	♂
28.	Length of respiratory horn	P
29.	Number of lateral spiracular openings on horn (sum of both horns)	P
30.	Number of apical spiracular openings on horn (sum of both horns)	P
31.	Width of apex of respiratory horn	P
32.	Length of operculum from base of *am* spine to tip	P
33.	Width of operculum at widest point	P
34.	Length of *am* spine	P
35.	Extent of opercular spinosity measured from base of *am* spine to distalmost teeth	P
36.	Extent of cleft in opercular spinosity measured from base of *am* spine to lowest point in submedian cleft	P
37.	Length of *ad* spine	P
38.	Length of d_1 spine	P
39.	Length of d_2 spine	P
40.	Length of d_3 spine	P
41.	Shape of *lpm* tubercles (0=spiniform, 1=semispiniform, 2=rounded)	P
42.	Shape of *lasm* tubercles (code as in *lpm*)	P
43.	Number of spiniform tubercles on penultimate abdominal segment	P
44.	Number of semispined tubercles on penultimate abdominal segment	P
45.	Number of abdominal segments with spiniform *lpm* tubercles	P
46.	Color of respiratory horn (0=lacking color, 1=pale yellow, 2=yellow, 3=light brown, 4=brown, 5=dark brown)	P
47.	Color of abdominal skin (code as in horn)	P

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THE UNIVERSITY OF KANSAS
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ON THE STATUS OF THE CAECILIAN *INDOTYPHLUS BATTERSBYI* TAYLOR

By

Edward H. Taylor

VOL. XLIX PAGES 337-344 DEC. 11, 1970 No. 5

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THE UNIVERSITY OF KANSAS
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Vol. XLIX Pages 337-344 Dec. 11, 1970 No. 5

On the Status of the Caecilian *Indotyphlus battersbyi* Taylor

Edward H. Taylor [1]

The genus *Indotyphlus* was proposed by me for a species of Caecilian from Khandala, Poona District, Bombay, India (Taylor, 1960). Three additional specimens were later found in the Bombay Natural History Museum and data taken from these were recorded by Taylor (1961, 1968). Recent acquisition of four specimens, EHT-HMS Nos. 6951-6954, from the "Bombay area" now permit further study, including the skull characters of the type-species, *I. battersbyi* Taylor.

Two other caecilian genera have representatives in this area. These are *Gegeneophis carnosus* Peters, a small species of comparable size and bearing a superficial resemblance to *I. battersbyi,* and *Ichthyophis bombayensis* Taylor, a large species, adults of which are at least double the length and three times the body width of *battersbyi* and having a longitudinal vent and a relatively long tail. The vent in the two preceding genera is transverse, and there is no tail.

The diagnosis of *Indotyphlus battersbyi* may be amplified as follows:

A slender species with head width somewhat less than the greatest body width. Body width contained in total length from about 45 to 53 times. Primary body folds vary from 130 to 144; secondary folds from 17 to 32, with 9 or 10 folds complete. Dental formula varies, but in the oldest (largest) specimens it is approximately 14-14 for the combined premaxillary-maxillary series, 17-17 prevomeropalatine, 12-11 dentary, and 2-2 for splenial. Teeth relatively large. Tentacular aperture in the adult fixed at a point twice as close to eye as to nostril, and in a nearly direct line between eye and nostril. Eye usually visible through the skin, in a socket that is continuous with the tentacular groove. Two nuchal collars more or less distinct, each with a dorsal transverse groove. Anal vent transverse; tail absent. Scales, in two or three rows posteriorly, in folds. Tongue with two well-defined black narial plugs. Large elongate recumbent glands especially prominent in posterior part of body.

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A prominent elongate cream-white spot present on sides of head, covering eye and tentacular aperture.

A skull prepared from EHT-HMS No. 6954 displays the following characteristics:

Skull proportionally longer than other caecilian skulls examined, being more than twice as long as wide (5.0 mm × 2.2 mm). The number of separate skeletal elements reduced as in other genera of the Caeciliidae.

The anterior dorsal part of skull covered by the nasopremaxillae which completely surround the nostrils. The lower anterior section of these elements narrowed below nostrils and along inner borders of nostrils, the median dorsal suture between the bones almost equal to their greatest length. Posteriorly they extend slightly between the following frontal bones. The common median suture between frontals considerably shorter than their lateral length. Frontals separated from parietals by a sinuous transverse suture. Parietals longer than frontals, their common suture about length of the bones, which are somewhat wider posteriorly than anteriorly. The foramen magnum surrounded by the posterior dorsal wings of the basisphenoid which form a short median suture.

On sides of skull posterior to the nasopremaxillae are the maxillopalatines which form the border of jaw behind; these followed by the squamosals which extend farther back bordering frontals and parietals above for some distance. Anteriorly squamosals notched by the eye sockets which are continuous with the large tentacular groove on the maxillopalatines. Quadrates attach to the posterior part of squamosals by long curving sutures. Stapes lying in a depression on the lateral part of basisphenoid, contacts both quadrate and pterygoid. A small spinelike anteriorly directed projection from basisphenoid passes above stapes.

Viewing the skull from the ventral (palatal) side, the basisphenoid is seen to cover most of the surface; posterior part, serving as part of braincase, somewhat inflated laterally. Immediately preceding this the element is much narrowed, then widens to form the "wings" which are scarcely discernable. The width diminishes gradually to about a point near posterior level of the internal nares where it becomes greatly narrowed, forming three anterior points, the median one separating prevomers for a very short distance.

Prevomers triangular, together occupying a diamond-shaped area about as wide as long. That on the right side bears 4 teeth, that on left, 3 teeth. Preceding these bones are the ventral parts of the nasopremaxillae, each bearing 5 teeth. These followed by the ventral parts of the maxillopalatine. The maxillary portion with 7 teeth and the palatine with 8 on right side (presumably the same on the left). Several replacement teeth of variable size present.

Dentaries 10-11, the larger anterior ones rather strongly hooked as well

Table 1. Data on *Indotyphlus battersbyi*. Measurements in mm.

Number (EHT-HMS)	6951	6952	6953	6954
Locality	"Near Bombay"	"Near Bombay"	"Near Bombay"	"Near Bombay"
Total length	208.	238.	212.	229.
Head width	3.2	3.2	3.2	3.2
Body width	4.6	4.9	4.5	4.6
Snout tip to 1st groove	4.4	4.8	5.0	5.0
Snout tip to 2nd groove	6.0	6.3	6.7	6.3
Snout tip to 3rd groove	7.7	8.	8.5	8.2
Tentacle to eye	0.56	0.6	6.4	0.65
Tentacle to nostril	1.3	1.3	1.3	1.3
Snout projects	0.75	0.8	0.6	0.6
Primary annuli	130	138	139	139
Secondaries	17	28	32	18
Complete secondaries	11	10	9	9
Premax-maxillary teeth	11-12	12-11	8-8	11-11
Prevom-palatine teeth	13-12	6-7	?-13	14-15
Dentary teeth	10-10	9-7	10-10	11-12
Splenial teeth	2-2	2-2	2-2	2-2
Width in length, times	45.2	48.5	47.1	50.

as being the largest teeth of all the series. Splenials, 2-2, the second tooth on each side being nearly directly behind first.

The greatly reduced numbers of the separate head bones separates this genus from the family Ichthyophiidae and associates it with the Caeciliidae, two genera of which also occur in India (*Gegeneophis* and *Uraeotyphlus*).

A male specimen, EHT-HMS No. 6951, had the anterior part of the snout from the region of the tentacle to the tip thickly covered with minute hair-like processes. Effort was made to photograph these, but they unfortunately do not show in the photograph (Fig. 1A). Much of the growth has been destroyed, since a rough touch serves to break or remove much of it. I suspect that this growth may be a temporary phenomenon, occurring during the breeding season. It is not visible on the other specimens.

The narial plugs on the tongue are strongly developed, and blackish in color. Their presence suggests that the species has a free swimming period at sometime in the life cycle.

A young specimen 115 mm in length having the following characters may or may not be of this species: EHT-HMS No. 6950, India. Data arranged as in Table 1. Length 115; 2.4, 3.8, 3.7, 4.6, 5.7, 0.2, 0.8, 0.9, 132, 24±, Dentition, 10-11, 12-11, 10-11, 1-?.

The specimen is light colored gray with a whitish area over the eye and tentacular aperture. The narial plugs on tongue are blackish.

The head is more rounded in lateral profile than in the described *Indotyphlus battersbyi*. The specimen has been in a preservative that has permitted an accumulation of crystals on many scales in the caudal region,

thus obscuring significant characters. Consequently, I am uncertain as to its placement.

I wish to acknowledge my obligation to Mr. R. Whitaker of Madras, India, and offer him my gratitude for making the new material available to me.

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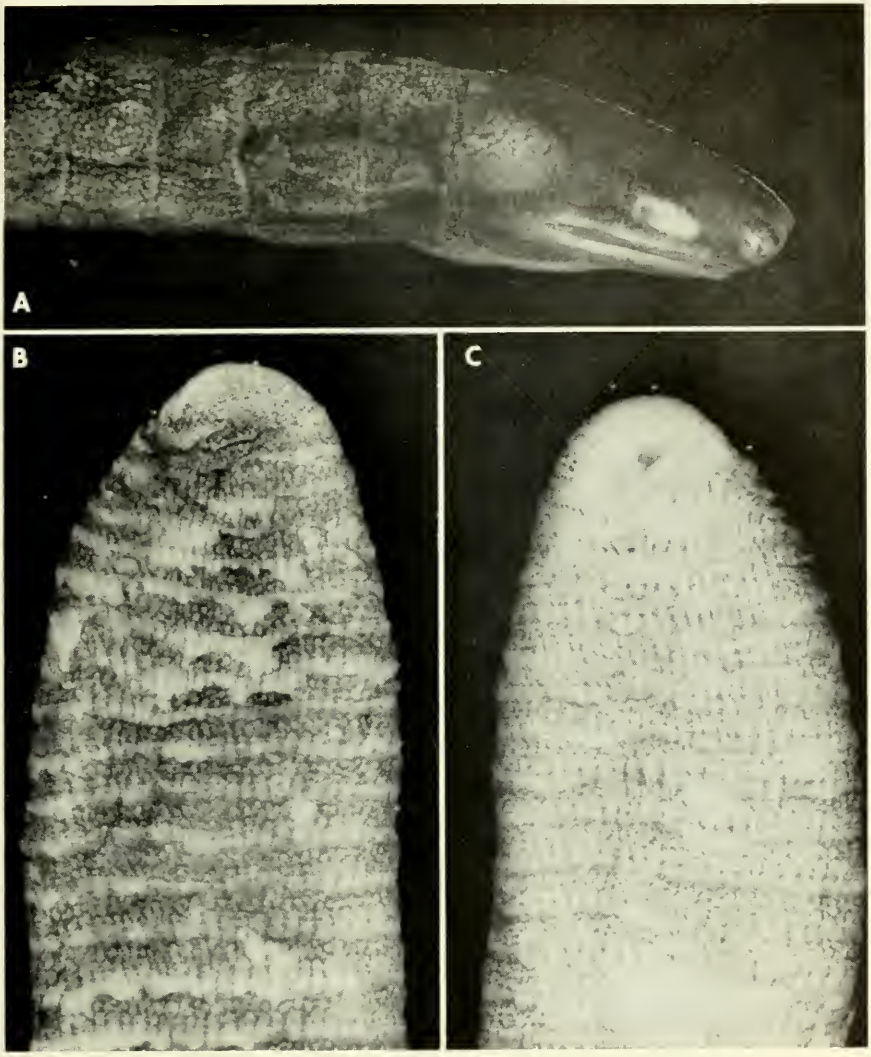

Fig. 1. *Indotyphlus battersbyi* Taylor, EHT-HMS No. 6951. A. Lateral view of head and neck (actual width of head, 3.2 mm). B. Dorsal view of terminal part of body showing glandular development under the skin. C. Same, ventral view, showing position of vent (distorted somewhat).

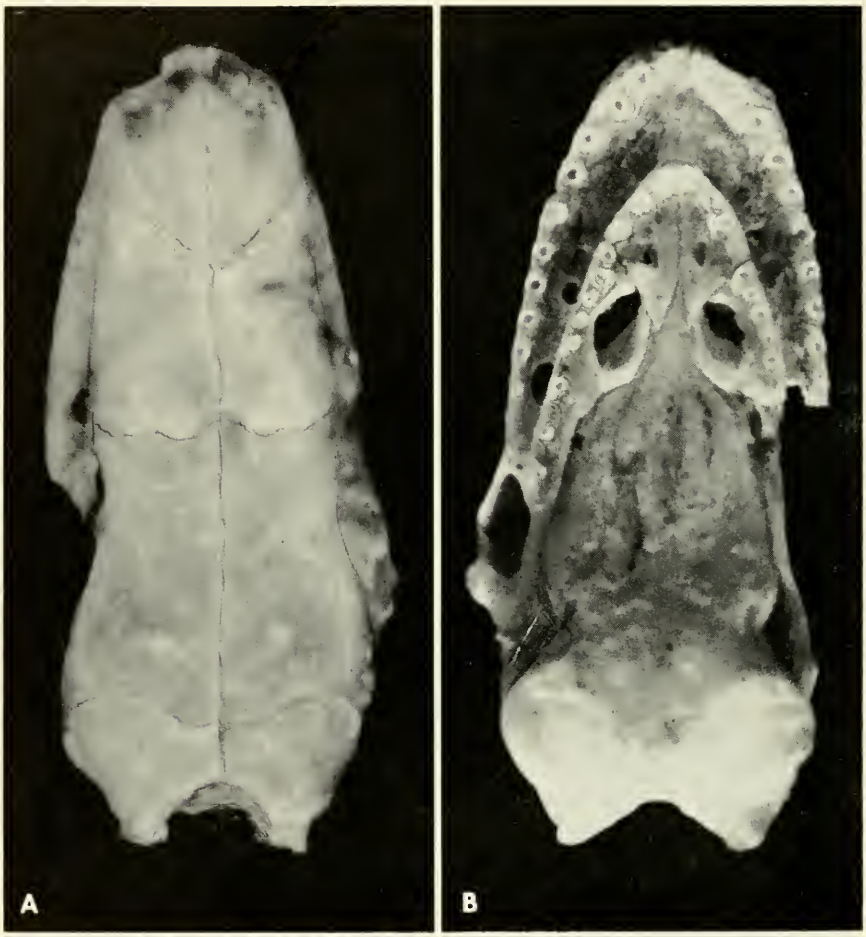

FIG. 2. *Indotyphlus battersbyi* Taylor, EHT-HMS No. 6954. A. Dorsal view of skull. B. Palatal view of skull. (Greatest length, 5 mm; width, 2.2 mm.)

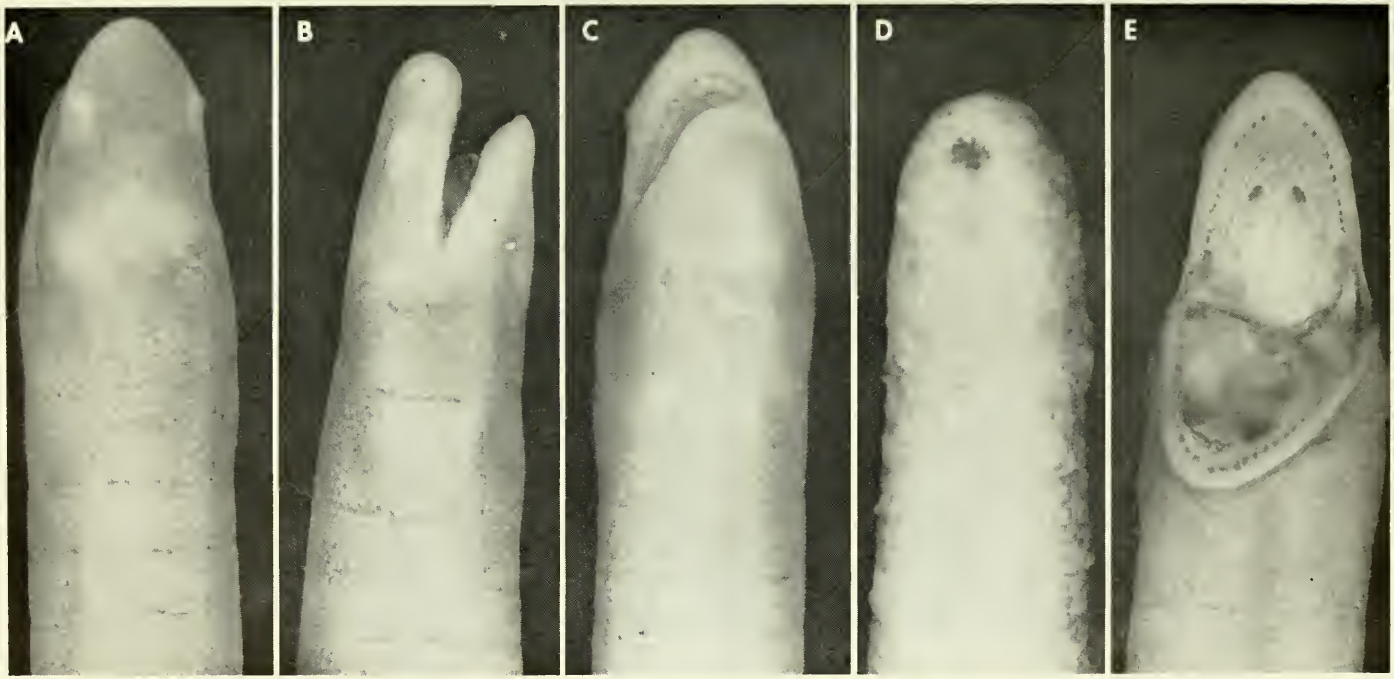

Fig. 3. *Indotyphlus battersby* Taylor ?, EHT-HMS No. 6950, young. A, B, C. Three views of head and neck. D. Subterminal region showing position of vent (distorted). E. Open mouth. (Actual width of head, 2.4mm.)

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INHERITANCE OF MULTIPLE HEMOGLOBINS IN TWO SPECIES OF WOODRATS, GENUS *NEOTOMA* (RODENTIA: CRICETIDAE)

By

Elmer C. Birney and Julio E. Perez

Vol. XLIX Pages 345-356 January 22, 1971 No. 6

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Inheritance of Multiple Hemoglobins in Two Species of Woodrats, Genus *Neotoma* (Rodentia: Cricetidae)

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The University of Kansas.

ABSTRACT

Hemoglobin samples of 171 woodrats of the species *Neotoma floridana* and *N. micropus,* and laboratory-bred hybrids of these two species, were studied by horizontal starch-gel electrophoresis. The patterns observed were grouped into seven categories or phenotypes. One hemoglobin phenotype was common to both species, three were present in *N. floridana* but not in *N. micropus,* two seen in *N. micropus* were not present in *N. floridana,* and one phenotype was unique to hybrids. Results of electrophoresing globins in urea-veronal starch demonstrated that all the variation observed resulted from differences in beta chains. Study of hemoglobins through as many as three generations of woodrats indicate that at least three beta loci are involved in the genetic control of woodrat hemoglobins. Tentative hypotheses are proposed to explain the inheritance patterns observed and a possible sequence for the evolution of multiple beta loci in woodrats.

INTRODUCTION

The woodrat species *Neotoma floridana* and *Neotoma micropus* are mostly allopatric in distribution and apparently behave in nature as good biological species, although they readily hybridize in the laboratory. *N. floridana* occurs from the eastern United States westward into the Central Great Plains, whereas *N. micropus* ranges from San Luis Potosí, México, northward as far as southwestern Kansas and adjacent Colorado (Hall and Kelson, 1959).

In the course of an extensive study to better elucidate the relationships of these two woodrats, it was found that both species are polymorphic in the ionographic properties of their hemoglobins as determined by horizontal starch-gel electrophoresis. Intraspecific variation of hemoglobins has long

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been known in humans and more recently has been reported in a variety of mammalian species including several of the rodent genus *Peromyscus* (Foreman, 1960, 1966; Rasmussen *et al.*, 1968). Because published information on the hemoglobins of *Neotoma* is not available and because we had a number of laboratory-bred woodrats of known parentage, we felt it worthwhile to study the inheritance of the observed polymorphisms.

ACKNOWLEDGMENTS

The completion of this investigation was made possible by the helpful suggestions and encouragement of numerous professors and students at The University of Kansas. Dr. Richard K. Koehn spent many hours helping us in the laboratory, suggesting methods of analysis, verifying results, and later reading the manuscript. Drs. J. Knox Jones, Jr., Robert Hersh, John A. Weir, and Raymond C. Jackson read the manuscript and gave constructive criticisms. Drs. Karl F. Koopman of the American Museum of Natural History and Robert J. Baker of Texas Tech University also read the manuscript and discussed the results and interpretations of the data with the senior author. The assistance of these and other colleagues is greatly appreciated. The authors, of course, assume full responsibility for the final interpretations and hypotheses.

Laboratory equipment and supplies were made available under a grant from the U.S. Public Health Service; woodrats were collected under the aegis of a Watkins travel grant to Birney from the Museum of Natural History, The University of Kansas; and the Kansas Academy of Science provided funds used to purchase feed for live woodrats. While working on the project, Birney was supported in part by National Science Foundation grant (GB-4446X) administered through The Committee on Systematic and Evolutionary Biology at The University of Kansas, and Perez by a Ford Foundation grant. We also thank Marcia Birney for typing the manuscript and helping to prepare the figures.

MATERIALS AND METHODS

Original stocks of woodrats were captured at the following localities (here specified only to county): *Neotoma floridana*—Cherry and Rock counties, Nebraska, and Douglas, Ellsworth, Ellis, Logan, and Finney counties, Kansas; *N. micropus*—Baca and Prowers counties, Colorado, and Barber, Meade, and Haskell counties, Kansas. Although individuals of three subspecies of *N. floridana* and two subspecies of *N. micropus* were studied, we are concerned herein only with variation and inheritance at the specific and interspecific levels. Animals were housed indoors in individual cages. Because breeding experiments were conducted for another purpose, matings were made without regard to hemoglobin phenotype. The woodrats used in this study later were prepared as museum specimens and cataloged in the Museum of Natural History, The University of Kansas. Thus, hemoglobin phenotypes can be correlated with individual specimens.

Hemoglobin samples were not studied from woodrats less than two months of age and no ontogenetic changes in hemoglobins were detected. Approximately 0.5 cc of whole blood was obtained by cardiac puncture, from an incision at the base of the tail, or from the suborbital canthal sinus. Blood was suspended immediately in 3 cc of 3.2% solution of trisodium citrate, pH 7.0, to prevent coagulation. After centrifugation, the citrate solution was

removed by aspiration and the cells washed three times in phosphate buffered saline, pH 7.0, lysed in about three times their volume of deionized water, and the hemoglobin solution separated from cell membranes by centrifugation.

Phenotypes of hemoglobins were determined by horizontal starch-gel electrophoresis. Gels were prepared using 16 grams of hydrolyzed starch in 125 ml of buffer that consisted of 0.2 M Tris and 0.025 M citric acid, pH 7.6. Samples were inserted into gels on Whatman number 3 filter paper. Buffer in the electrode reservoir consisted of 0.3 M sodium borate, pH 8.6. Electrophoresis was conducted at 25v/cm at room temperature for 90 minutes, the gels removed, sliced, and both halves stained in a saturated solution of amido black in water-methanol-glacial acetic acid (5:5:1). At the beginning of the study, half the preparations were stained by the benzidine method (50 ml of water, 0.1 ml of 30% hydrogen peroxide, 0.25 ml acetic acid, and 100 mg benzidine dihydrochloride), but this procedure was discontinued when it became evident that both techniques demonstrated the same pattern. The iodoacetimide method described by Riggs (1965) was used to investigate the possibility that some or all of the hemoglobin patterns observed were artifacts resulting from polymerization.

The 6 M urea-0.1 M veronal method of Chernoff and Pettit (1964) was used to determine whether variation was in the alpha (α) or beta (β) chains of hemoglobin molecules. Globins were prepared by cold acid-acetone precipitation, and redissolved in the urea-veronal buffer containing mercaptoethanol. Horizontal electrophoresis was run at 4° C for 22 hrs at 25v/cm. Urea-veronal buffer, pH 8.0, was also used in electrode reservoirs. Following electrophoresis, gels were sliced and both halves stained with amido black. In all cases, gels were destained in repeated rinses of the stain solvent.

RESULTS

The hemoglobin phenotypes of 171 woodrats, including members of both species and their hybrids, were determined. These animals were involved in 35 matings in which the phenotypes of both parents were known and 18 matings in which the phenotype of only one parent was known (Table 1). Hemoglobin patterns were grouped into seven categories or phenotypes, designated A through G (Fig. 1). Groupings were made according to the number and position of major bands without consideration of diffuse zones and minor bands. For the sake of completeness, the status of diffuse zones and minor bands is included in the description of each phenotype; their patterns and characteristics generally were consistent in the hemoglobin pattern of an individual and probably represent genetic differences, but because there was considerable variation in these characters when all animals were considered, interpretation was not possible. Major bands of four different migra-

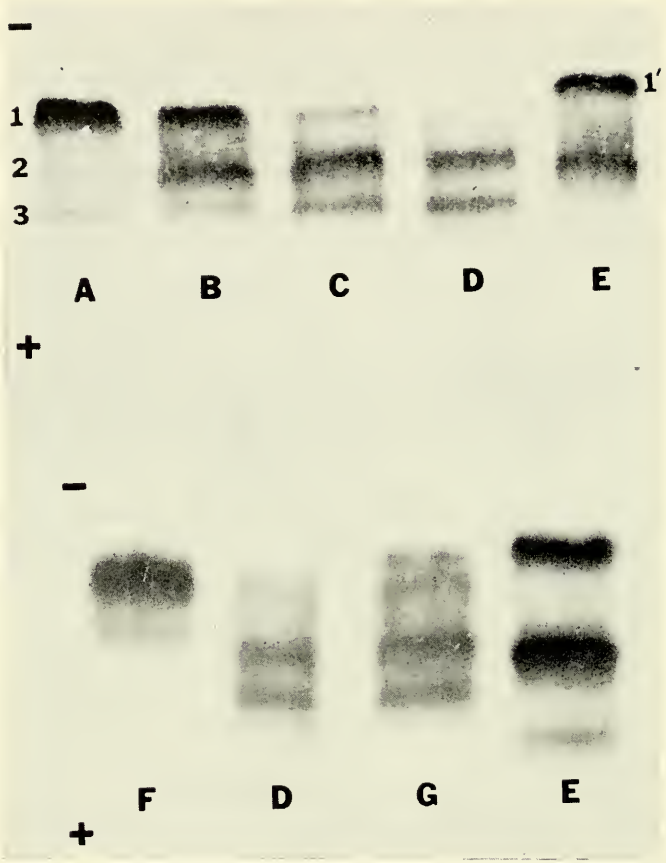

FIG. 1. Starch gels showing electrophoretic patterns of woodrat hemoglobins. Phenotypes are indicated by letter, cathode by a minus sign, and anode by a plus sign. The points of insertion of the samples are out of view at the cathodal end of each gel.

tion distances were observed. These were labeled 1′, 1, 2, and 3, with 1′ having the slowest and 3 the fastest rate of migration. Minor bands were observed in some individuals of both species at position 3 and another faint band was seen in some *N. micropus* and some hybrids near the leading edge of the diffuse zone at a position designated 4.

Phenotype A consisted of band 1 and a leading diffuse zone that terminated in a minor band at position 3. Only five *N. micropus* demonstrated this pattern. Phenotype B, observable as major bands 1 and 2 preceded by a diffuse zone, was the most common phenotype in *N. floridana* and was not uncommon in *N. micropus* and hybrids. The diffuse zone was slightly longer in *N. micropus* than in *N. floridana* and a minor band sometimes occupied position 3 (Fig. 1B). A minor band also was present occasionally at

position 4 in the B phenotype of *N. micropus* and hybrids. Phenotype C had major bands at positions 1, 2, and 3, whereas D had only bands 2 and 3 and a trailing diffuse zone that terminated at the level of position 1 in *N. floridana* but extended to position 1′ in some hybrids. Position 3 was never occupied by a major band in the phenotypes of *N. micropus*, thus limiting phenotypes C and D to *N. floridana* and hybrids. Phenotype E consisted of bands 1′ and 2 with a long leading diffuse zone that usually contained a minor band at position 4. It was difficult in a few cases to identify a sample either as E or B, but an attempt to establish an intermediate category was unsuccessful. This problem and its ramifications will be discussed below in more detail. Because band 1′ was never found in *N. floridana*, phenotype E occurred only in *N. micropus*, where it was the most common phenotype observed. Two *N. floridana*, neither of which was involved in laboratory matings, were the only animals having phenotype F. This phenotype consisted of a single broad band and a small leading diffuse zone. The proteins that formed the band migrated slightly more slowly than proteins normally forming band 1, but not so slow as those of band 1′. Assignment of this band to category 1 is open to question; however, because only two individuals of the phenotype were observed and because no other *N. floridana* had band 1′, it seems more parsimonious to consider it as band 1. Phenotype G, which was seen only in four hybrids, sometimes appeared to have all four major bands. On other occasions a hemoglobin sample from the same individual rats would show only bands 1′, 2, and 3.

Phenotypic patterns of samples treated with iodoacetamide and electrophoresed in the Tris-borate system did not differ from those of untreated samples. Globins electrophoresed in the urea-veronal system showed no variation in the cathodal fractions, but variation was present in anodal fractions (Fig. 2).

DISCUSSION

Chernoff and Pettit (1964) summarized the technique of electrophoresing globins in a urea-veronal system containing mercaptoethanol. Urea dissociates the polypeptide chains of hemoglobin and mercaptoethanol prevents disulfide bridging of reactive -SH groups. In this system, human alpha polypeptides migrate toward the cathode and human beta polypeptides migrate toward the anode. If it is assumed that hemoglobins of woodrats behave in a similar manner, our results indicate that variation observed in the hemoglobins of *Neotoma* is in the beta chains. This is generally consistent with situations in other mammals, including humans (see Ingram, 1963, for review), where variation is known in α-chains but to a lesser extent than in β-chains. Variation in both α and β chains also has been reported for orangutans, genus *Pongo* (Sullivan and Nute, 1968). House mice of the genus *Mus*

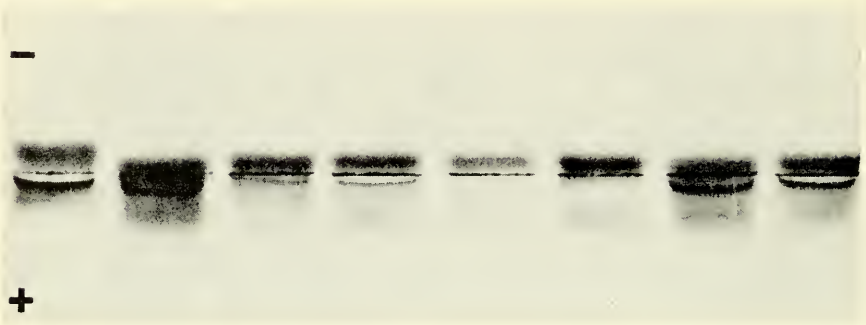

FIG. 2. Electrophoretic patterns of globins in urea-veronal starch. The sample to the left is human globin, probably human A. Reading left to right, subsequent samples are woodrat globins from animals having phenotypes C (*N. floridana*), B (*N. floridana*), B (*N. micropus*), A (*N. micropus*), E (*N. micropus*), C (*N. floridana*), and B (*N. floridana*). The cathode is indicated by a minus sign and the anode by a plus sign.

are known to have at least two β-chain variants that affect electrophoretic patterns of hemoglobin (see Lush, 1967, for review) and two α-chain variants that affect solubility (Hutton *et al.*, 1964).

Glucksohn-Waelsch (1960) proposed that the beta locus of *Mus* has undergone duplication to produce two or more closely linked beta loci. We found that when all phenotypes of *Neotoma* were considered there was no position consistently occupied by a band. It therefore appears that the same hypothesis may be valid for the control of hemoglobin production in woodrats. Foreman (1966) discussed variation in hemoglobins of *Peromyscus gossypinus* in terms of an animal being either homozygous or heterozygous for a given multibanded phenotype. In attempting to interpret our data in a similar fashion, we noted that all matings of phenotype B $\times$ B resulted only in progeny of phenotype B. This indicated that B might represent a homozygous condition. It was thought that D might be the other homozygote in *N. floridana* with C representing the heterozygous condition. No D $\times$ D matings were available for study, but results of B $\times$ C and B $\times$ D matings indicate that B does not always represent a homozygous condition because one D progeny resulted from a cross of the former (only B and C progeny should have been observed if B is always homozygous) and five progeny of phenotype B and two of phenotype D were observed in 15 offspring from the latter cross. Furthermore, such a hypothesis does not account for the presence in natural populations of phenotypes A and F, which lack band 2, and E and G, which have band 1′. It is necessary, therefore, to consider genetic control of hemoglobin production in woodrats in terms of the alleles controlling each electrophoretic band.

In the two species studied, variation in major bands can be explained in terms of either two or three beta loci for *N. micropus* and three beta loci for

TABLE 1. Summary of hemoglobin phenotypes of parental woodrats (*Neotoma*) and their laboratory-born progeny.

Phenotypes of parents	Identification of parents	Number of matings	Number of progeny	Number of progeny of each phenotype						
				A	B	C	D	E	F	G
B × B	floridana × floridana	3	8	0	8	0	0	0	0	0
	floridana × micropus	3	6	0	6	0	0	0	0	0
	micropus × micropus	2	2	0	2	0	0	0	0	0
	hybrid × hybrid	1	2	0	2	0	0	0	0	0
	Totals	9	18	0	18	0	0	0	0	0
B × C	floridana × floridana	2	8	0	5	3	0	0	0	0
	floridana × micropus	1	2	0	1	0	1	0	0	0
	Totals	3	10	0	6	3	1	0	0	0
B × D	floridana × floridana	4	9	0	3	5	1	0	0	0
	floridana × hybrid	1	2	0	1	1	0	0	0	0
	micropus × hybrid	1	1	0	0	0	1	0	0	0
	hybrid × hybrid	1	3	0	1	2	0	0	0	0
	Totals	7	15	0	5	8	2	0	0	0
B × E	micropus × micropus	2	5	0	2	0	0	3	0	0
C × C	floridana × floridana	3	8	0	2	2	4	0	0	0
C × D	floridana × floridana	4	13	0	0	10	3	0	0	0
C × E	floridana × micropus	1	1	0	0	0	0	0	0	1
D × E	floridana × micropus	3	8	0	0	0	3	2	0	3
	micropus × hybrid	1	1	0	0	0	1	0	0	0
	hybrid × hybrid	2	4	0	0	0	0	4	0	0
	Totals	6	13	0	0	0	4	6	0	3
? × B	floridana × floridana	3	4	0	4	0	0	0	0	0
	floridana × micropus	1	2	0	2	0	0	0	0	0
	micropus × micropus	2	5	0	3	0	0	2	0	0
	micropus × hybrid	1	2	0	2	0	0	0	0	0
	Totals	7	13	0	11	0	0	2	0	0
? × C	floridana × floridana	2	4	0	1	2	1	0	0	0
? × D	floridana × floridana	2	3	0	0	1	2	0	0	0
? × E	micropus × micropus	7	18	5	0	0	0	13	0	0
Grand totals		53	121	5	45	26	16	25	0	4

N. floridana. Both species apparently have separate loci producing the proteins that form bands 1 and 2, and *N. floridana* has a third locus for production of the β-chain of the protein that forms band 3. Whether or not the minor band formed at this position by some *N. micropus* implies that the same locus is present in this species is not known. If the same locus is involved, the protein produced is clearly in lower concentration in *N. micropus* than in *N. floridana*. The presence of a minor band at position 4 in some *N. micropus* indicates that this species has another locus not present in *N. floridana*. Bands 1′ and 1 either may be alleles of each other or band 1′

may be controlled by a locus not present in *N. floridana;* if allelic, the 1′ allele occurs naturally only in *N. micropus.*

In several matings (see Table 1) it was noted that one or more progeny lacked a band that was formed by the hemoglobin of both parents, but any position occupied by a band in the progeny was always occupied in at least one parent. Our data are not conclusive, but they do indicate that alleles we have termed β^0 (no peptide produced) are involved in the hemoglobin inheritance of *Neotoma.* Such a non-functional "allele," which may be either a deleted area on the chromosome as discussed below or an area that is physically present but for some reason (being under the control of modifier genes, for example) does not contribute a peptide chain, was proposed and designated $H\beta\ I^0$ to explain inheritance of hemoglobins in *Peromyscus maniculatus* (Rasmussen *et al.,* 1968). Harris *et al.* (1959) suggested that a similar allele, Hp^0, might exist in association with normal haptoglobin alleles in a human family. A "silent" gene also has been proposed (see Heyworth and Firth, 1967) to explain the absence of serum-cholinesterase in children of parents that both produced the enzyme; Ashton (1958) and Gahne (1964) explained the absence of slow-α 2 plasma protein in cattle with a "silent" S^0 allele. In *Neotoma,* β^0 alleles seem to occur at all of the beta loci, but such a hypothesis makes possible three hypothetical phenotypes for *N. floridana* (bands 2 and 3 singly observed, and bands 1 and 3 together) and two for *N. micropus* (band 1′ alone and band 2 alone) that were not observed in this study.

In some cases, at least, gene duplication probably results from small unequal cross-overs of homologous chromosomes so that one chromosome contains both loci and the other no longer has the locus in question (see Fig. 3). In the case of *Neotoma,* the chromosome without a beta locus may be lethal and thus lost from the population, or it may remain to act as a β^0 in the inheritance of hemoglobin. Certainly two such chromosomes would be lethal for an individual, but one conceivably could be carried in association with a functional homologue. In any event, it is the chromosome bearing the duplicated locus that is of most interest because it now would contain a beta locus free to mutate with a high degree of impunity. Even if altered in a manner that would be advantageous to the population, however, the chromosome capable of stimulating production of two forms of polypeptide chains would probably take a considerable period of time to become fixed in a population or species. During this period, woodrats having one "new" or altered chromosome paired with one of the unaltered form would be heterozygous for the new beta peptide. If duplications and mutations of this type have occurred twice during the evolution of these two species of woodrats, the variation and inheritance patterns of the major electrophoretic bands can be explained.

Table 2 shows a series of combinations of alleles that will explain the

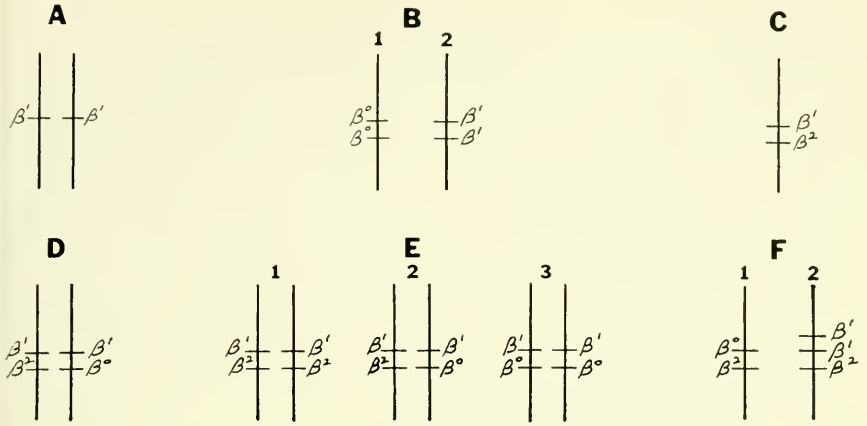

FIG. 3. Hypothetical sequence showing evolution of beta loci in *Neotoma*. Vertical lines are diagramatic representations of the chromosomal portions supporting beta loci, which are depicted by horizontal lines. A, "original" diploid condition of an individual having unduplicated loci; B, possible arrangements of beta loci after a small unequal crossover; C, condition after one locus of chromosome 2 mutates; D, the "new" chromosome pairs with an unaltered chromosome resulting in woodrats heterozygous for β^2; E, three diploid conditions of progeny resulting from a mating of two heterozygotes; F, possible arrangement of beta loci after another crossover.

hemoglobin variation seen in *N. floridana* together with the phenotypes of animals having each pair of chromosomes. The relative frequencies of phenotypes in natural populations does not approach that seen in the table. This suggests that some of the hypothetical combinations do not exist, or that some combinations exist in higher frequencies than others. Most likely both situations are true. A similar interpretation of possible chromosomal combinations can be made for *N. micropus,* except that in this species locus number three is absent and locus number one either has three alleles (β^0, $\beta^{1'}$, and β^1) or there is another locus controlling band 1′.

As indicated above, the relationship between $\beta^{1'}$ and β^1 is not clear. When two forms of hemoglobin molecules having mobilities nearly the same are present, it is possible that they usually migrate together with the faster form either being held back to the speed of the slower or "dragging" the slower along with it. The occasional occurrence of both bands in some runs of phenotype G hemoglobin suggests (1) that a woodrat can produce both peptides, (2) that these can separate during electrophoresis, and (3) that when they do not separate 1′ is present and band 1 is absent. Three intraspecific matings of *N. micropus* with one B parent and one E parent (Table 1) failed to help answer this question because the genotypes of the parents were unknown. In one case both progeny were B, in another all three progeny were E, and in the third litter one offspring was B and two were E. However, interspecific matings (Table 1) involving individuals of *N. floridana* (which

TABLE 2. Seven possible combinations of beta alleles on chromosomes of *Neotoma floridana* showing the resultant phenotypes of individuals having a given pair of chromosomes.

	$\beta^1\ \beta^2\ \beta^3$	$\beta^1\ \beta^2\ \beta^0$	$*\beta^1\ \beta^0\ \beta^3$	$\beta^1\ \beta^0\ \beta^0$	$\beta^0\ \beta^2\ \beta^3$	$\beta^0\ \beta^2\ \beta^0$	$*\beta^0\ \beta^0\ \beta^3$
$\beta^1\ \beta^2\ \beta^3$	C	C	C	C	C	C	C
$\beta^1\ \beta^2\ \beta^0$	C	B	C	B	C	B	C
$*\beta^1\ \beta^0\ \beta^3$	C	C	**	**	C	C	**
$\beta^1\ \beta^0\ \beta^0$	C	B	**	F	C	B	**
$\beta^0\ \beta^2\ \beta^3$	C	C	C	C	D	D	D
$\beta^0\ \beta^2\ \beta^0$	C	B	C	B	D	**	D
$*\beta^0\ \beta^0\ \beta^3$	C	C	**	**	D	D	**

* No evidence that such a combination exists.

** Phenotype not observed.

never have the $\beta^{1'}$ allele) and those of *N. micropus* with phenotype E frequently resulted in progeny having band 1′. These animals necessarily were heterozygous, having received the $\beta^{1'}$ gene from the *micropus* parent and either a β^1 or β^0 from the *floridana* parent. This clearly demonstrates that animals having band 1′ can be heterozygous, and suggests that the $\beta^{1'}$ allele usually acts as a dominant, either by influencing the mobility of molecules containing polypeptides produced at the β^1 locus or by inhibiting the production of such polypeptides.

Only the G phenotype was unique to hybrids of the two species. This pattern resulted only when one parent, either a *micropus* or hybrid, had band 1′ and the other, either a *floridana* or hybrid, had band 3. Observation of a "hybrid" phenotype having bands 1′, 2, and 3 was expected. However, as discussed above, we had not predicted that band 1 would occur in association with 1′.

The three B × C matings (Table 1) are of special interest. Six of the 10 progeny from these matings were phenotype B, three were C, and one was D. The fact that more were phenotype B than C possibly can be attributed to the small sample, but the occurrence of a D individual necessitates that the C parent was heterozygous for band number 1 and that a chromosome (one of the pair in the B parent, which was a *micropus*) exists with the combination of alleles $\beta^0\ \beta^2\ \beta^0$. This combination in the homozygous condition would yield a phenotype having a single major band occurring in the number 2 position. No individual having such a phenotype was observed. Other evidence for the existence of the $\beta^0\ \beta^2\ \beta^0$ chromosome can be derived from the six D × E matings studied. It was expected from the model that most of the progeny would be either phenotype C or G. Phenotype C, however, was not observed in the 13 progeny and only three were of phenotype G. The six E progeny could result only if the D parent was genotypically $\beta^0\ \beta^2\ \beta^3$ and $\beta^0\ \beta^2\ \beta^0$. The E parent of the four offspring of phenotype D must have been $\beta^{1'}\ \beta^2\ \beta^0$

and β^0 β^2 β^0. It is of further interest to note that in five of these six crosses two or more progeny were studied and in each case all progeny of a litter had the same phenotype. The meaning of this is not clear and more D × E crosses would be enlightening. It should be reiterated that such matings were possible only when both species were involved in the ancestry because in non-hybrid rats band 1′ is present only in *N. micropus* and band number 3 only in *N. floridana*. Matings of C × D rats were conducted four times and the expected preponderance of offspring having the C phenotype (10C:3D) was observed. None of the progeny demonstrated phenotype B, which would have necessitated the β^0 β^2 β^0 combination in the D parent and a C parent heterozygous for band 3.

Any cross involving either an A or an F parent would be instructive. We twice attempted to make an A × A mating but were unsuccessful.

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ECOLOGY OF A POPULATION OF THE GREAT PLAINS SKINK *(EUMECES OBSOLETUS)*

By

Russell J. Hall

VOL. XLIX PAGES 357-388 FEB. 18, 1971 No. 7

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Ecology of a Population of the Great Plains Skink (*Eumeces obsoletus*)[1]

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ABSTRACT

An intensive three year investigation of population dynamics was conducted. On an area of several acres near Lawrence, Kansas, 324 individuals were captured 751 times; captures made elsewhere in the same general region brought the number of records available to 1751.

The species inhabits rocky, open hillsides in eastern Kansas. This type of habitat is common in the region of the study, but in most situations it is unstable and probably would persist for only a few years in the absence of disturbance such as results from grass fires or heavy grazing.

The skinks are active from mid-April to early October. The number of skinks trapped is closely correlated with temperature. A body temperature between 31.5 and 35.0° C is necessary for maintenance of normal activity. Disability occurs below 15° C and above 42° C. However, the skinks have the capacity to regulate their temperatures by contact with sun-warmed rocks. Each individual confines most of its activity to a familiar home range. The average size of home range varies from approximately 0.02 to 0.20 acres, depending on the method by which it is calculated.

Recapture of marked individuals has indicated patterns of growth through the fifth year of life. Males possess motile sperm early in the third year of life. Females are more variable, breeding first in their third or fourth year. On the average, respectively 25%, 63% and 80% of the females breed in their third, fourth, and later years. Clutches averaging 11.5 eggs are laid in June or July. Realized fecundity averages about 50% of the calculated reproductive potential.

Heavy mortality occurs in the early years of life, but the survival rate exceeds those of most small vertebrates. The mean life-expectancy is nearly 1.5 years at hatching. High rate of survival is correlated with relatively large size, fossorial habits, low vagility, and the brooding habit. The relatively low reproductive potential of the species is also correlated with its high rate of survival. Predation does not seem to be an important cause of mortality.

INTRODUCTION

An intensive study of a local population of the Great Plains skink, *Eumeces obsoletus,* was undertaken because it appeared that populations of this species would yield information unlike that obtained from the study of other species. The species is more fossorial and more secretive than most

[1] Extracted from a thesis submitted to the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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species studied previously and it seems to differ from them demographically. While not easily observed, the skinks can be captured in their shelters or trapped with reasonable success. Other features that have facilitated the study of this species are its abundance near Lawrence, Kansas, and the excellent background material provided by a previous study (Fitch, 1955) on the species' habits and adaptations.

The present report is largely based on data accumulated in the years 1966-1968. In three years of field work, a population of Great Plains skinks was studied intensively. Additional data were obtained from laboratory studies of captive individuals, from records collected at the University of Kansas Natural History Reservation in the years 1948-1968, and from numerous records of captures made on nearby areas. Of records obtained from the Natural History Reservation, 634 were the basis of Fitch's (1955) report, but these have been subjected to further analysis. A total of 1751 records for 895 individual skinks was available at the time of this report. However, most information was obtained from one population in which 324 individuals were captured 751 times.

The most comprehensive reference on the ecology of *E. obsoletus* is Fitch's (1955) study. His paper summarizes the literature on the species to that date, includes a description of the species and its geographic range, and presents the results of a field study which was cut short by the decline and eventual extirpation of the local population under study.

Other studies of the ecology of skinks of the genus *Eumeces* include those of Breckenridge (1943) on *E. septentrionalis,* Fitch (1954) on *E. fasciatus,* Tanner (1957) on *E. skiltonianus,* and Mount (1963) on *E. egregius.* Few generalizations can be made on the basis of these studies, except that larger species and those with ranges farther north seem to have the lowest reproductive potentials. Studies of other genera of skinks, including species of *Lygosoma* (Brooks, 1967), *Leiolopisma* (Barwick, 1959), and *Emoia* (Alcala and Brown, 1967), have shown these small lizards to differ considerably in ecology from *E. obsoletus* and from species of *Eumeces* in general.

Studies of iguanids including *Sceloporus olivaceus* (Blair, 1960), *S. undulatus* (Crenshaw, 1955), *Uta stansburiana* (Tinkle, 1967a, b), and *Crotaphytus collaris* (Fitch, 1956) have shown these lizards to have high reproductive potentials and generally high annual rates of turnover. Similarly, studies of teiids including *Cnemidophorus sexlineatus* (Fitch, 1958a) and *Ameiva quadrilineata* (Hirth, 1963) have shown high annual mortality. Zweifel and Lowe (1966) studied *Xantusia vigilis* and found this sluggish, viviparous species to have a lower rate of reproduction and a higher rate of survival than that known for any other species of lizard. These studies of lizard ecology have shown great variations in life history and have shown *E. obsoletus* to be somewhat unique among temperate zone lizards in being

larger than most species, reproducing more slowly, and presumably having a much lower mortality rate.

ACKNOWLEDGMENTS

Special recognition is due to Dr. H. S. Fitch who ably directed the study and made data in his care available to me. Other persons helping in various ways during the study were Drs. W. E. Duellman, D. R. Clark, Jr., D. H. Janzen, J. D. Lynch, H. W. Shirer, and N. A. Schappelle, and Messrs. A. C. Echternacht and R. R. Fleet. My wife, M. E. Hall aided in preparing the manuscript. Financial aid from the Department of Zoology and the Graduate School of the University of Kansas and from the Kansas State Biological Survey facilitated parts of the study.

METHODS

Skinks were captured primarily by live trapping or by hand while they were inactive in their shelters. Traps used were of a new design (Hall, 1967) but were similar in operation to the funnel traps used in other studies. Traps were placed near natural obstructions, so that they might intercept skinks moving about the surface. Dangers to entrapped lizards from predators or from overheating were minimized by shielding the traps with rocks and by daily inspection of traps during hot weather. The number of traps in operation was gradually increased to total 27 in October, 1966; 59 in May, 1967; and 81 in May, 1968. In all, 285 records (38% of the total number of captures on the study area) were obtained by trapping. Captures by hand of skinks that were moving on the surface provided valuable information concerning patterns of activity, but such captures were relatively rare and comprise a small proportion of the total. Most hand captures were of lizards that were inactive in their burrows beneath flat rocks. Trapping and capture by hand complemented each other somewhat. Trapping was most successful when the temperature was high, owing to the increased activity of the lizards, and capture by hand was most successful in the spring when low temperatures prevented much surface activity.

Individuals captured were routinely processed at the site of capture and then immediately released to minimize the adverse effects of captivity. Captured skinks were marked by the removal of toes. No more than one toe was removed per foot and toes were removed from no more than three limbs on any skink. The handicapping involved was apparently slight.

Snout-vent length was recorded to the nearest millimeter, as was the length of the tail, with original and regenerated portions measured separately. Lizards were weighed with a spring scale after being secured with a small rubber band.

Circumstances of capture, including observations on activity and weather were recorded. When possible, body temperature was taken with a Schul-

theis rapid indicating thermometer, as was the temperature of the lizard's surroundings. Additional notes recorded pertained to sex, reproductive condition, ectoparasitism, and method of capture.

In recording the locality of capture, prominent natural landmarks were used. Localities were recorded by compass reading and estimated distance with reference to these landmarks.

A chamber providing a uniform and reliable temperature gradient was constructed for study of temperature relations. It was 1.8 m long, 17.5 cm wide and 30 cm high. The aluminum floor was heated by five 250 watt infrared heat lamps, each controlled by a thermostat sensitive to about 1-2°C. In operation, the floor of the chamber was covered with one cm of sifted soil which was maintained at a temperature range from 22°C to 54°C. Experimental animals were acclimated for at least 24 hours to the chamber before heating it, and to the heated chamber for at least one hour before testing was begun. Other studies on thermal relations involved cooling skinks in salted ice water and then observing them as they warmed, and heating individuals in a small battery jar with a suspended heat lamp.

Dissection of specimens collected from areas near the study area revealed the presence of mature sperm in males and enlarged ova in females. In addition, females handled in the field were palpated to reveal the presence of enlarged ova. In late May and June, gravid females were distinguished by their distended flanks and the reliability of this criterion was established by numerous dissections. Males in reproductive condition were distinguished by eversion of the hemipenes which emitted a cohesive mass of semen in mature individuals.

DESCRIPTION OF THE STUDY AREA

Most of these studies were confined to the population of one area. The area is located about 3 miles south and 8 miles west of Lawrence (section 36, township 13S., range 18E.), Douglas County, Kansas. The land is used as a pasture for dairy cattle of the Fred Flory farm, and is about 20 acres in area. However, the entire pasture was not suitable habitat for *E. obsoletus* and most study was confined to the area along two concentric rock outcrops, representing a plot 1800 feet long and 500 feet wide.

The southern third of the area is part of the floodplain of Washington Creek, a tributary of the Wakarusa River. The deep, alluvial soil supports a good stand of smooth brome *(Bromus inermis)*. To the north, approximately 50 feet higher than the alluvium, is a terrace with thin soil, broken by protruding rocks. On the slope between the terrace and the alluvium, is an outcropping of limestone of Pennsylvanian age, the Toronto Limestone of the Oread Escarpment (O'Connor, 1960). The outcrop consists mostly of rubble, with few large blocks present. The rock is hard and brittle and has

Fig. 1. A portion of the study area showing the flat rocks and herbaceous vegetation characteristic of most of the area.

fractured often in its lateral plane, producing many flat fragments. North of the terrace is another outcrop which rises 50 feet above the former and differs in having more massive boulders, many of which have not broken away from the parent stratum of Leavenworth Limestone of the Oread Escarpment. This rock seems less compact than that of the lower outcrop and fractures irregularly, leaving more massive boulders which are studded with sharp projections. Soil on the cuesta is thicker than that of the terrace and supports more luxuriant growth of grasses.

The conformation of the scarp on the study area is that of a spur, with the upland forming a finger-like projection into the valley. Drainage of the upland accumulates in a small stream, appearing in the floodplain. In years of normal rainfall, the stream is permanent.

The abrupt change in topography over the scarp has a profound effect on the vegetation. The thinness of the soil, the movement of rock in its semi-fluid matrix, and constant erosion by running water tend to keep the area in a state of perpetual disturbance. Nevertheless, human disturbance seems to have had the greatest effect in shaping the land as it exists today. Wells (1965) noted that escarpments in the Great Plains tend to be wooded; in

eastern Kansas it is rare to find an unwooded scarp that does not bear evidence of human disturbance. The low, herbaceous vegetation of the study area (Fig. 1) seems to have been maintained by continuous disturbance. Grazing, bulldozing and application of herbicides were observed during the present study.

Although the climax woodland has been removed from the study area, grasses have failed to replace it completely, especially along the rock outcrops. Here, with the few trees present, is growth of rank, weedy vegetation including sunflower *(Helianthus)*, vervain *(Verbena)*, and mullein *(Verbascum)*. A list of plant species present would include numerous agricultural pests, many of them notorious as indicators of overgrazing.

Certain of the plants seem to favor the population of skinks. Species providing shade and aiding in conservation of moisture include Hackberry *(Celtis occidentalis)*, Osage Orange *(Maclura pomifera)*, American Elm *(Ulmus americanus)* and Red Mulberry *(Morus rubra)*. Each is represented by few individuals, but collectively they have a pronounced effect on the environment. Plants frequently used by the skinks for shelter are Osage Orange, Annual Sunflower *(Helianthus annuus)*, Mullein *(Verbascum thapsus)* and Coralberry *(Symphoricarpos orbiculatus)*.

The study area was chosen primarily for its high population of skinks. A secondary consideration was the relative isolation of the area suitable as habitat for *E. obsoletus*. Although no physical barriers surrounded the plot, none of the adjacent areas provided favorable habitat for them.

BEHAVIOR AND SPATIAL RELATIONSHIPS

Cycles of Activity

Seasonal activity in *E. obsoletus* is shown in part by the phenological events recorded in Table 1. Close correspondence from year to year is indicated in most events, although the three years differed in patterns of temperature and moisture. Appearance of eggs and hatchlings was exceptionally late in 1967, possibly because of unusually cool and moist conditions that year.

Activity is initiated by males somewhat earlier in the spring than by females. This pattern in shown in Tables 1 and 2. For chi-square tests in

Table 1. Observed phenology in the years of the study.

	1966	1967	1968
First Male	March 14	March 11	March 16
First Female	March 28	April 3	April 3
First Four Females	April 21	April 8	April 8
First Eggs	June 15	June 22	June 18
First Hatchlings	July 15	July 31	July 18
Last Record	October 2	September 23	....

Table 2, it has been assumed that individuals should appear in each monthly sample in proportion to their relative abundance as determined from the entire yearly sample. It was against this expected result that the observed numbers were tested.

Table 2. Frequency of capture by sex throughout the season of study.

	1966			1967			1968		
	Females	Males	X^2	Females	Males	X^2	Females	Males	X^2
March	1	1	..	0	22	***	0	2	..
April	17	54	***	10	85	***	26	69	***
May	20	15	ns.	26	50	**	45	43	ns.
June	13	19	ns.	36	31	ns.	42	35	ns.
July	5	3	ns.	46	34	ns.	31	15	**
August	16	7	*	10	7	ns.	12	9	ns.
September	6	3	ns.	..	..	..	..	..	..

* P = 0.05, ** P = 0.01, *** P = 0.001, ns. = not significant.

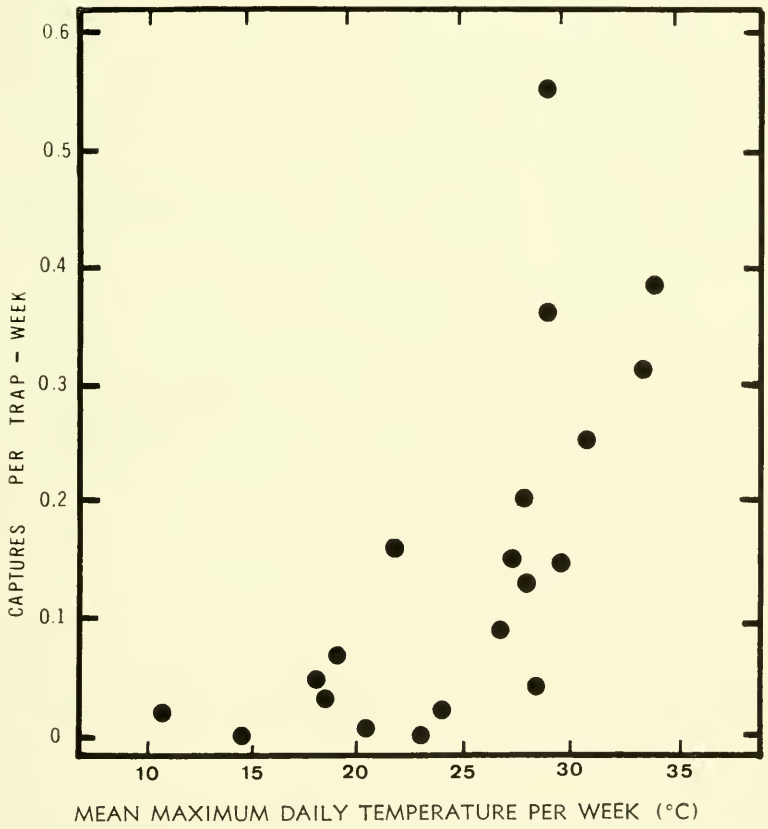

Fig. 2. Relation between captures per trap per week and the mean maximum daily temperature per week in 1967.

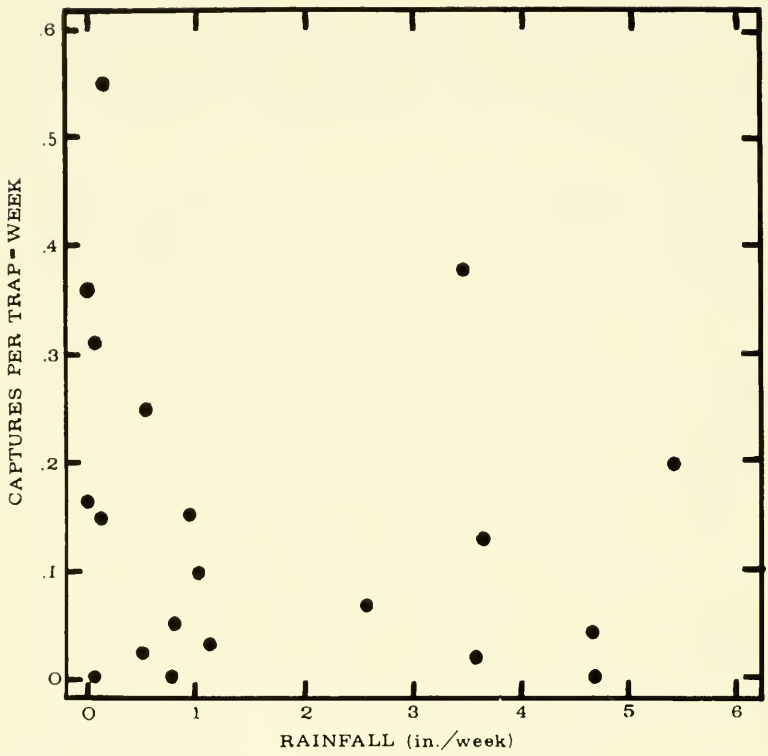

FIG. 3. Relation between rainfall and activity in the 1967 season.

Although major events in the annual cycle of the species seem to be largely independent of yearly weather variations, surface activity, as represented by trapping records, shows a close fit with short term local variations, as is illustrated in Figures 2, 3 and 4. The effect of temperature is most noticeable and that of rainfall least noticeable. The effect of rainfall is difficult to assess because varying amounts of rainfall can saturate the upper strata of the soil. The influence of date is actually an integration of temperature, moisture and perhaps differences in the behavior of the animals. Thus, none of the apparent trends can be substantiated without experimental isolation of the variables.

Skinks in nature are usually observed on the surface between 10:00 a.m. and 4:00 p.m. CST if the temperature is high enough for their emergence. Captive individuals follow a similar pattern. If the temperature is below 30°C, they do not emerge.

THERMAL RELATIONS

Several hundred records of body temperatures were obtained in the field. They are of three principal types: Temperatures (1) of individuals found in

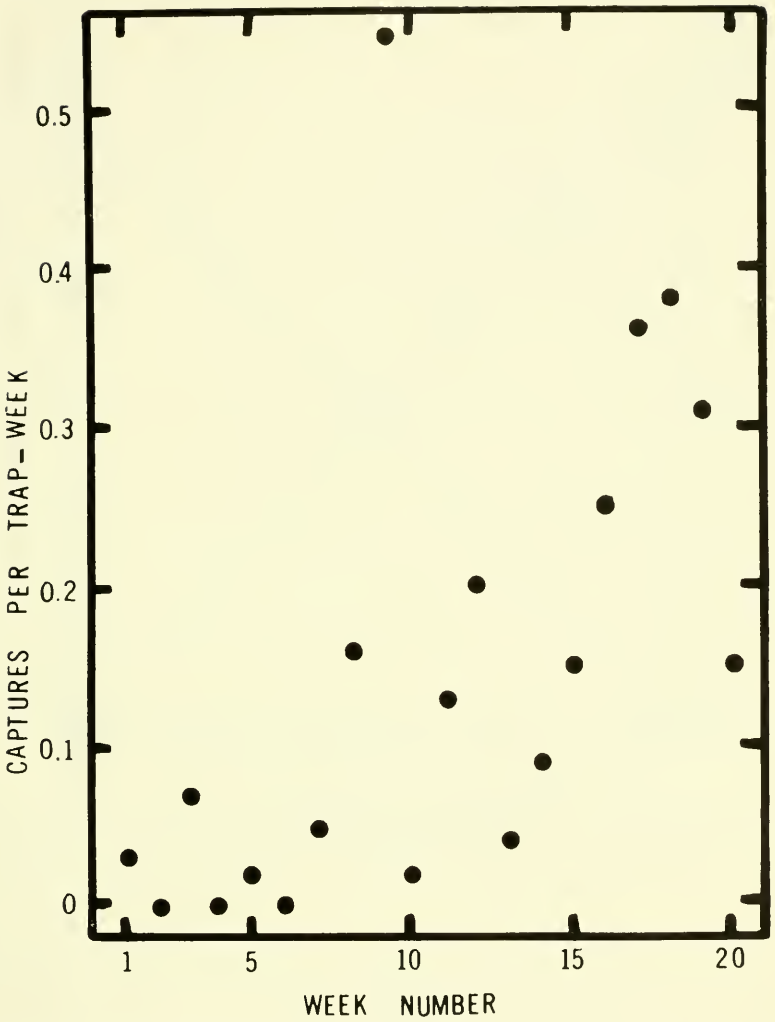

Fig. 4. Correlation between activity and time in 1967. Records included begin in the week of April 16 and end with the week of August 27.

burrows, (2) of those found active in the open, and (3) of those confined in traps. Only the first two types have been used (Figs. 5 and 6). Temperatures were obtained for only 15 individuals found active in the open. The range of these temperatures was 26.4-36.8°C with a mean of 31.62±1.03°C. For nine of these records, corresponding records of air temperature are available. The mean temperature of the skinks was 29.96±1.36°C and the mean air temperature was 25.09±1.26°C, a noticeable but insignificant difference.

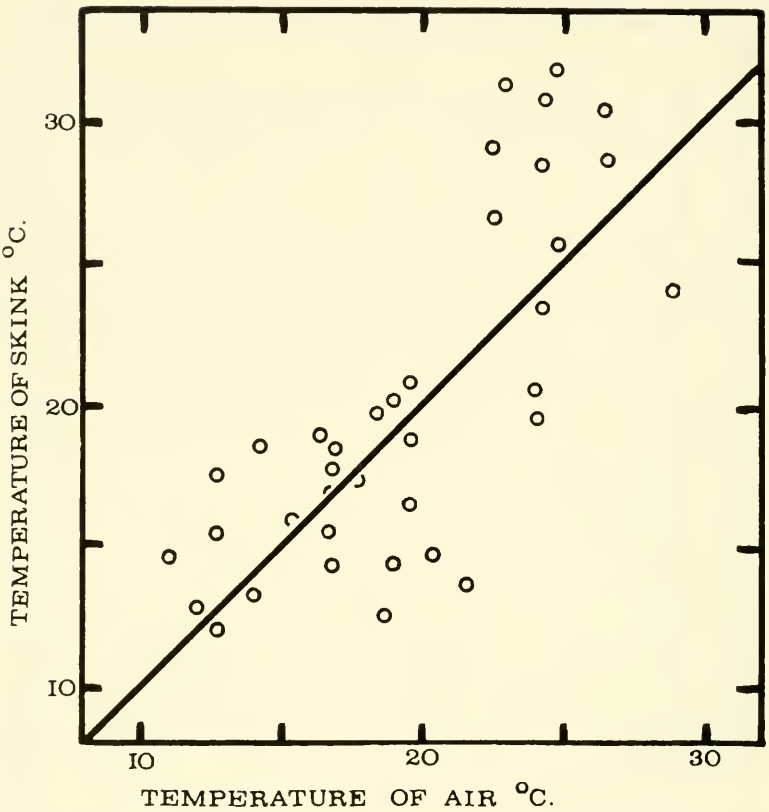

FIG. 5. Correlation between temperatures of skinks found in shelters and the contemporaneous air temperature. The diagonal line represents identity between the two temperature readings.

Relationships examined in the laboratory were those defined by Cowles and Bogert (1944) as the lethal minimum, critical minimum, voluntary minimum, normal activity range, maximum voluntary tolerance and critical maximum. Two of Cowles and Bogert's categories, the basking range and the lethal maximum, were not investigated.

Determination of the normal activity range and its variations was accomplished with the thermal gradient chamber. Only animals that were moving about actively were considered, and these could be classed in three categories: (1) those within the normal activity range and not thermoregulating, (2) those seeking cooler surroundings, and (3) those seeking warmer surroundings. The mean of temperatures so recorded should represent the midpoint for normal activity and the range should bracket its extremes (Tab. 3). Allowing for the inability of individuals to regulate their temperatures continuously, the activity range can be delimited roughly between

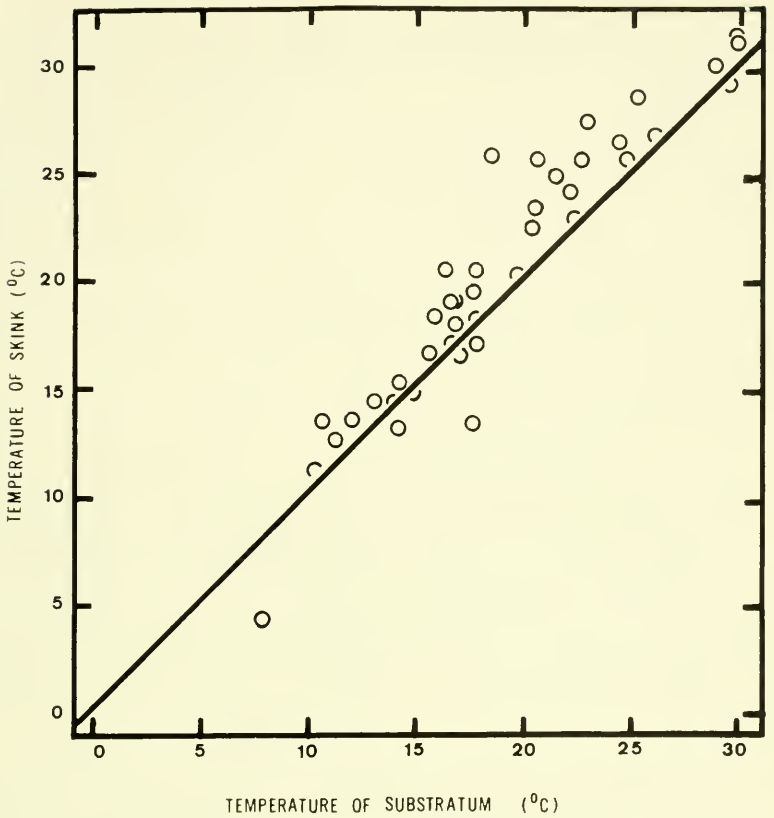

Fig. 6. Correlation between temperatures of skinks found in shelters and temperatures of the soil surface of the burrows. The diagonal line represents identity between the two temperatures.

Table 3. The temperature range of normal activity.

	N	Mean Temp. °C	Range
Juveniles	8	33.5 ± 0.4	32.5-35.8
Adult Males	13	33.7 ± 1.1	31.0-35.0
Adult Females	9	32.3 ± 0.4	30.7-34.6
Total Sample	30	33.2 ± 0.3	30.7-35.8

31.5 and 35.0°C. As with other thermal parameters, the lower limit of this range is much less sharply defined than the upper limit.

To investigate the voluntary minimum, temperatures of all individuals found burrowing at the cold end of the gradient chamber were recorded. The temperature ranges (Tab. 4) overlap the normal activity range and their mean approximates the lower limit of the normal activity range. Other

TABLE 4. Body temperatures of individuals engaged in low temperature burrowing.

	N	Mean Temp. °C	Range
Juveniles	10	30.9 ± 0.8	27.2-33.7
Adult Males	11	28.5 ± 1.2	23.8-33.4
Adult Females	15	30.9 ± 0.9	26.5-36.1
Total Sample	36	30.2 ± 0.6	23.8-36.1

TABLE 5. Differing thermal responses at differing periods in the daily cycle.

Time Interval (P.M., CST)	12:00-1:00	1:00-2:00	2:00-3:00	3:00-4:00	4:00-5:00
Number of Observations	8	8	28	16	11
Mean Temp. of Observations °C	30.0	32.1	32.4	31.3	31.4
Proportion Burrowing	0	0.12	0.21	0.31	0.64

observations (Tab. 5) suggested by the work of Regal (1967) indicate that the tendency for low temperature burrowing varies during the daily cycle.

The critical minimum was observed by cooling animals in ice water, removing the torpid individuals, and prodding them continuously as they warmed. Cloacal temperatures at first movement and at the first locomotion were recorded. Temperatures of first movement (N=8) averaged 13.3°C (range: 10.2-17.8). Temperatures of first locomotion (N=12) averaged 15.5°C (range: 12.4-21.0) and this latter average approximates the critical minimum.

The lethal minimum was not determined because of the difficulty in ascertaining the temperature at death. However, in preliminary experiments, two individuals withstood body temperatures of −2°C for 10 minutes and recovered fully.

The maximum voluntary temperature, indicated by convulsive efforts of warming individuals to escape, was obtained for animals placed in a battery jar and warmed by a heat lamp. Twenty observations on two subadult and two adult males indicated a maximum voluntary temperature of 37.0°C (range: 35.1-38.6). Some error may have resulted from a time lag between actual discomfort on the part of the lizards and the recording of body temperatures.

In other experiments, the four individuals used above were heated until locomotor disability occurred. The mean temperature for this was 41.9°C (range: 41.2-42.4). This was accepted as the critical thermal maximum. All animals recovered and showed no immediate ill effects from overheating.

HOME RANGE AND MOVEMENTS

In the present study, 128 skinks were captured at least two times each. However, 20 individuals showed no measurable movement between cap-

Table 6. Calculated size of home range as it relates to the number of captures per individual—minimum polygon method—records of all adults included.

Number of Captures	Calculated size of Home Range (ft^2)	Range	Number of Animals
3-4	289.4	10-1144	24
5-6	1127.2	104-1350	10
7-8	1072.8	390-1831	4
9-10	2139.0	887-2964	3
11+	2598.0	618-5224	4

Table 7. Mean distance moved between successive captures for male, female, and juvenile individuals.

	N	Mean Distance Moved (ft)	Range	Calculated Home Range (ft^2)
Males	127	33.31 ± 2.31	3-143	3484.0
Females	87	32.72 ± 8.21	3-120	3361.6
Juveniles	59	27.88 ± 3.28	1-97	2430.7

Table 8. Mean maximum distances moved by males, females and juveniles.

	N	Mean Maximum Distance Moved (ft)	Range
Males	44	52.36 ± 4.92	6-143
Females	29	47.62 ± 6.32	6-120
Juveniles	35	33.00 ± 4.40	1-97

tures and their records have been omitted from the calculations because they convey the false impression that skinks do not move between successive captures at the same locality. Six individuals moved distances greater than 150 feet and these were judged to involve movements outside the home range and have also been omitted. Thus, records of 102 skinks captured a total of 273 times are available for calculation of the size of the home range.

The minimum polygon method involves estimating the home range from the area encompassed by the outermost points of capture. The calculated size of the home range when this method is used (Tab. 6) is strongly related to the number of times individual animals are captured.

A second method of estimating the sizes of home ranges has been employed by Fitch and others (Hayne, 1949a). The mean of distances moved between successive captures (Tab. 7) is found and is used as the radius of a circle which is taken as the size of the home range. Occassionally, the mean maximum distance moved (Tab. 8) has been expressed as a measure of the vagility of a species.

Probability density function involves finding the mean radius of recapture and adding to it two standard deviations to describe the radius of a circle within which 95% of all movements will occur. Mean radii of recap-

TABLE 9. Mean radii of recapture.

	MALES			FEMALES			JUVENILES		
	Mean Radius of Recapture (ft)	No. of Radii	No. of Animals	Mean Radius of Recapture (ft)	No. of Radii	No. of Animals	Mean Radius of Recapture (ft)	No. of Radii	No. of Animals
All Animals	20.36 ± 4.12	177	42	19.37 ± 1.70	126	30	17.41 ± 1.40	104	27
Those Captured:									
Two Times	18.80 ± 2.78	30	15	11.00 ± 3.91	14	7	18.17 ± 2.39	42	14
Three Times	19.53 ± 4.18	30	10	16.22 ± 1.60	27	9	9.88 ± 2.94	18	6
Four Times	12.04 ± 1.36	24	6	17.50 ± 4.24	16	4	23.50 ± 6.65	4	1
Five Times	28.80 ± 1.10	5	1	21.75 ± 3.62	20	4	18.27 ± 3.74	15	3
Six Times	30.06 ± 3.81	18	3	16.08 ± 3.54	12	2	15.33 ± 0.94	6	1
Seven Times	13.43 ± 2.45	7	1	35.14 ± 5.69	7	1	....	..	..
Eight Times	15.12 ± 6.72	8	1	44.75 ± 7.03	8	1	38.37 ± 4.16	8	1
Nine Times	21.06 ± 3.25	18	2	....	..	..	....	..	..
Ten Times	....	..	..	33.60 ± 5.78	10	1	....	..	..
Eleven Times	19.27 ± 1.75	11	1	25.55 ± 4.39	11	1	9.36 ± 1.64	11	1
Twelve Times	21.50 ± 6.21	12	1	....	..	..	....	..	..
Fourteen Times	29.64 ± 3.97	14	1	....	..	..	....	..	..
All Captured Five-Fourteen Times	23.27 ± 1.64	93	11	27.21 ± 2.16	68	10	19.40 ± 2.19	40	6

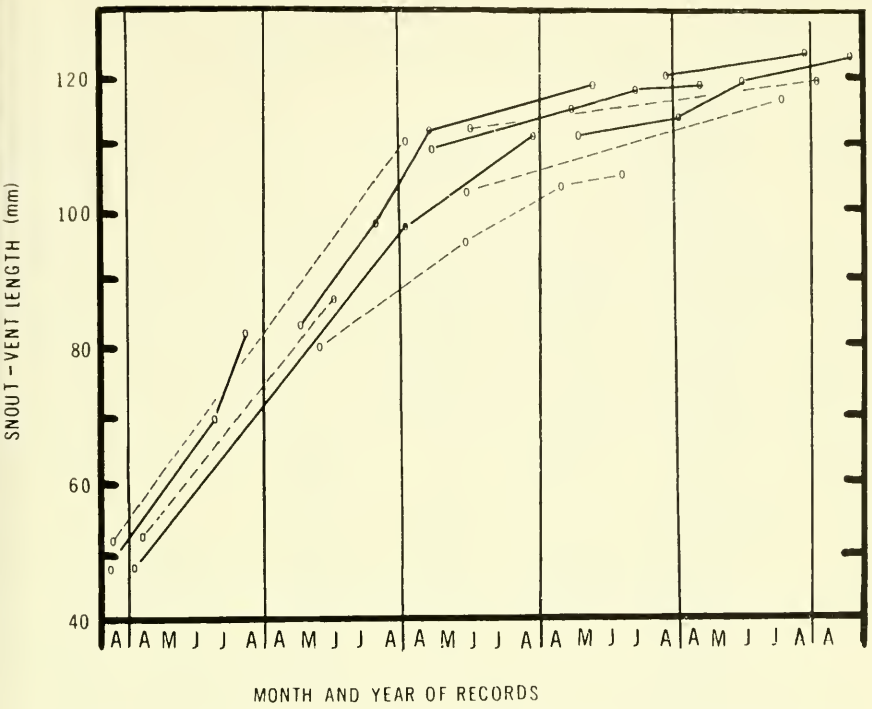

Fig. 7. Records of growth selected on the basis of long timespan between recorded captures. Growth in males is represented by solid lines while growth in females is represented by dotted lines.

ture, determined graphically, are recorded in Table 9. The different estimates tend to be relatively constant despite a slight tendency for the radius to become larger as the number of captures increases. This tendency may be a function of elapsed time, with slight shifts in home range accounting for the longer movements.

POPULATION DYNAMICS

Growth and Age Classes

Because growth records of individuals extend over a 28 month period of trapping and because most three year olds are recognizable on the basis of size, it has been possible to distinguish age groups through the fifth year (Fig. 7). Age classes have been delineated to provide a minimum of overlap in size between successive groups. In the rare instances in which growth falls outside the expected limits, individuals in question have been assigned to the older of possible age classes on the assumption that retardation of normal growth is more common than acceleration. The average rate of

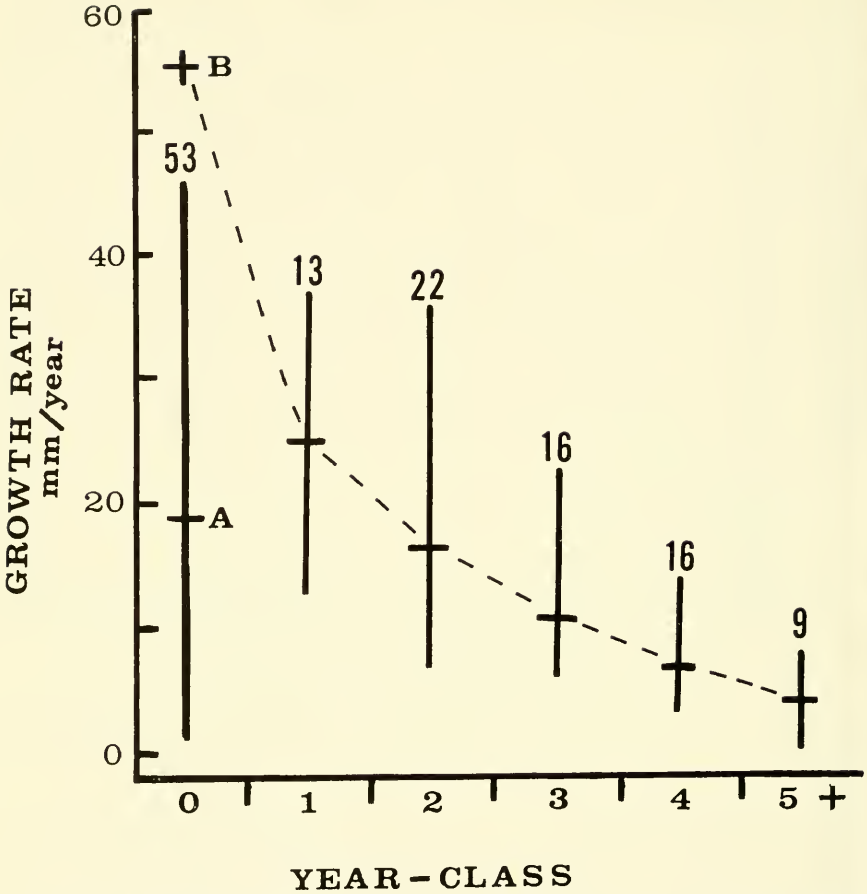

FIG. 8. Mean rate of growth per year, plotted for individuals recaptured within one week of one full year from the date of a previous capture. The mean rate of growth for hatchlings during the relatively short period of activity of their first season of life is indicated by A while B represents the extrapolated growth rate per full season of activity. Horizontal bars represent means, vertical bars represent ranges, and the numbers above them are sample sizes.

growth for different age classes (Fig. 8) is based on records spanning a full year. Although there is great individual variation, a pattern of decelerating growth is clearly indicated. Catastrophic events and natural stresses might result in lack of growth, and thus these methods underestimate the age of some individuals. On the other hand, activities of capturing and marking animals might tend to retard growth and calculated growth rates might have been too low with ages overestimated, but this is considered unlikely.

Skinks were captured as early as March 11 and as late as October 3, but growth appears to be negligible except in May, June, and July. Even within

Table 10. Rates of growth (in mm per year) relative to age and intactness of tail. Numbers in parentheses are sample sizes.

	Age (Years) 1-2	2-3	3-4
Tail Intact	26.0 (6)	14.9 (9)	10.0 (7)
Tail Broken	24.2 (7)	17.6 (11)	11.1 (9)

these months of greatest activity, growth is variable. Ten randomly chosen recapture records, each spanning more than a week, but all within the specified months, had the following mean rates of growth in mm per day: April, 0.032; May, 0.148; June, 0.191; July, 0.245; August 0.101; September, 0.050.

The tail, when intact, may comprise 20% of a lizard's weight. It would seem that regeneration of all or part of the tail would retard growth of the remainder of the body, but apparently this is not true except possibly for yearlings (Tab. 10).

Reproduction

Observation of motile sperm in males has confirmed that they are sexually mature when they emerge from their third hibernation at an approximate age of 32 months. At this time they average 102 mm in snout-vent length.

In 1966, nine females 97-126 mm in length were collected early in the activity season. The smallest of those containing enlarged ova was 105 mm in body length and close to the size of the smallest female found brooding eggs in a natural nest. The age of these females, as projected from Figure 7, is approximately 32-34 months. In the same sample, an individual of 97 mm snout-vent length, also considered to be a third year female, possessed many small ova, all less than 2 mm in diameter. Some of the older females contained enlarging ova while others did not.

On the study area in 1966, 16 females of adult size were captured between May 15 and July 15, and 12 were judged to be gravid. Five out of 8 third-year females were gravid, all of 4 fourth year females were gravid as were 3 of the 4 individuals in the fifth and subsequent years of life.

In 1967, the first gravid females were noted June 12 and the last on June 22. Of 10 adult females captured in this interval, only 3 of them were gravid. Three year olds were somewhat stunted in growth in 1967 and are thought not to have become fecund.

In 1968, between May 13 and June 18, 36 adult sized females were captured. Eighteen (50%) of them were gravid (1 of 16 three year olds, 8 of 15 four year olds, and 9 of 11 of fifth year and older females).

Mating activity in captive animals has been observed on April 13 and May 9 (1966) and May 3 (1968). Instances of gregariousness which are usually associated with mating were observed in the field on May 7 and

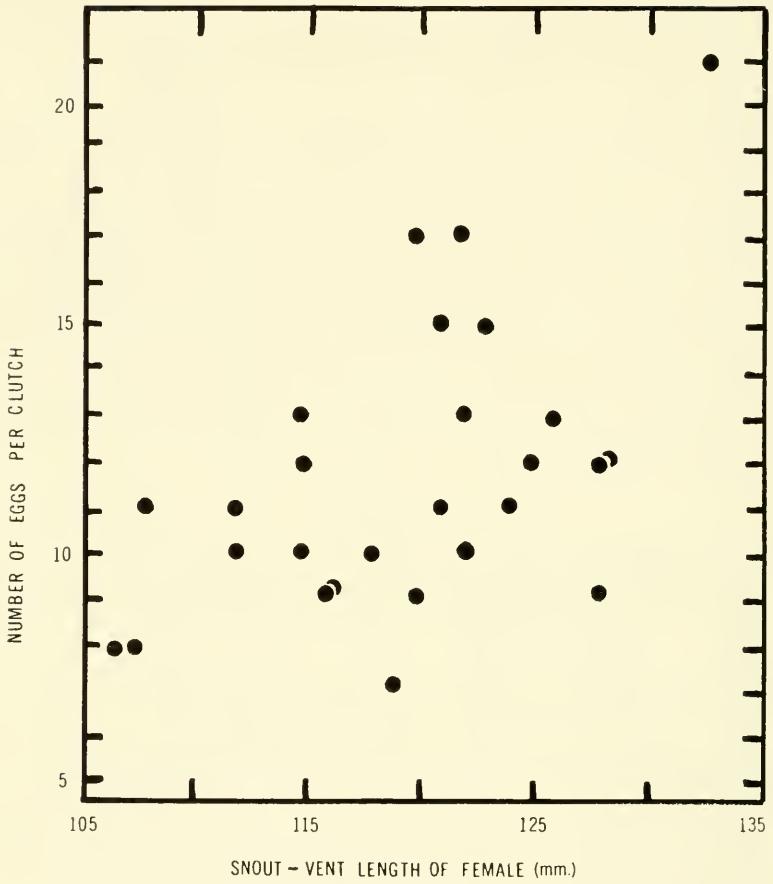

FIG. 9. Correlation between the snout-vent lengths of fecund females and the number of eggs per clutch.

May 18 (1967) and on April 19, May 10, May 13 (two instances), and May 15 (1968).

Counts of eggs have been taken from clutches laid in captivity, clutches found in natural nests and, in two instances, from oviducal eggs dissected from freshly-killed females. In all, 18 counts were obtained. In addition, counts of 12 clutches from the vicinity of my study are available (Fitch, 1967). For the 30 counts thus available, a mean clutch size of 11.5 is represented (range: 7-21 eggs per clutch). The most frequently occurring clutch sizes are 10 and 12. There is some indication of a positive correlation between clutch size and snout-vent length (Fig. 9).

The possible eating of eggs by brooding females may cause some error in my estimates of clutch size because some of the nests were discovered long

Table 11. Reproductive potential estimated for the years of the study.

Year	Age Class		Total No. Present	Age-Specific Fecundity	Reproductive Potential
1966	3yr	0.56		8.5	153.0
	4yr	0.29	34	10.1	101.0
	5+yr	0.15		13.1	65.5
	Total				319.5
1967	3yr	0.45		8.5	137.7
	4yr	0.41	36	10.1	149.1
	5+yr	0.14		13.1	65.5
	Total				352.3
1968	3yr	0.44		8.5	160.0
	4yr	0.32	45	10.1	144.4
	5+yr	0.24		13.1	154.6
	Total				459.0

after laying. Comparisons of the mean sizes of clutches found early in development and those recorded later have revealed no differences, however.

Growth data and mean clutch size provide a measure of age specific fecundity. Limitations on the accuracy of the measures are similar to those affecting the determination of age groups. Four three year old females produced clutches averaging 8.5 eggs, and 9 four year olds produced clutches averaging 10.1 eggs. Fifteen clutches of females five years old and older had a mean size of 13.3 eggs.

To estimate the reproductive potential of the population, data were accumulated on population structure and total numbers of adult females present in the central part of the study area, an area that was sampled with nearly equal effort in each of the years of study. The total population of adult females in this area ranged from 34 to 45 (Tab. 11). Although the difference in numbers seems large (a 32% range) it may be explained by the yearly differences noted in population structure. Such differences seem to result from varying successes of reproduction in different years.

Reproductive potential was calculated by multiplying the number of females present by the age specific fecundity (Tab. 11). The estimates of reproductive potential may be somewhat misleading because varying proportions of three year olds had reached breeding maturity. Some three year olds were known to have bred in 1966 and 1968, but limited data indicated that most three year olds were not mature in 1967.

To obtain estimates of egg production for each of the years of study, the age specific reproductive potentials have been multiplied by the estimates of age specific breeding frequencies. An exception is 1967 when poor reproduction and correspondingly meager data prevented obtaining separate statistics for the different age groups. Estimates of realized fecundity are summarized in Table 12. Observations of the numbers of hatchlings present subsequently tended to confirm the calculated patterns of fecundity.

TABLE 12. Estimates of realized fecundity for the years of the study.

Year	Age Class	Reproductive Potential	Proportion Breeding	No. of Eggs Produced
1966	3yr	153.0	0.625	140
	4yr	101.0	1.0	101
	5+yr	65.5	0.75	48
	Total	319.5	0.75	289
1967	Total (4 & 5+)	214.5	0.43	92
1968	3yr	160.0	0.06	10
	4yr	144.4	0.53	77
	5+yr	154.6	0.82	116
	Total	459.0	0.56	203

SURVIVORSHIP

Two methods of determining survivorship have been attempted in the present study: calculation from the age structure of the population, and calculation from the direct observation of rates of survival from year to year.

Deevey's (1947) third method for calculating survivorship requires determination of the age structure of the population. It is based on two assumptions: (1) all age classes can be sampled with equal efficiency, and (2) reproductive success does not vary from year to year. Although successfully employed by Zweifel and Lowe (1966) in their study of *Xantusia vigilis*, there are indications that the necessary assumptions cannot be made in the present study.

Age structure obtained by direct observation (*i.e.* the number of individuals actually marked) is shown (Fig. 10) for the population for three consecutive years. Data are reasonably complete only for 1966 and 1967 and results for these two years have been averaged and appear also in Figure 10. As indicated, poor reproductive success in some years seems to have affected these average figures. Of more concern are the effects of the method in representing age structure. This method may severely underestimate numbers in the younger age classes because of the difficulty in observing them. Mortality is greatest in these lower age classes, and most individuals are observed only after the critical period has been passed. Hence, the method may grossly misrepresent the patterns of mortality.

Estimation of population size may be made with the Hayne (1949b) index. Hayne applied this index to samples obtained over a short period of time, thus minimizing the effects of immigration, emigration, and mortality. The relatively slow accumulation of data in the present study necessitated using sampling periods that covered the entire season of activity and consequently the Hayne estimates are probably not good indicators of population size. Also, they appear to give poor indications of age structure,

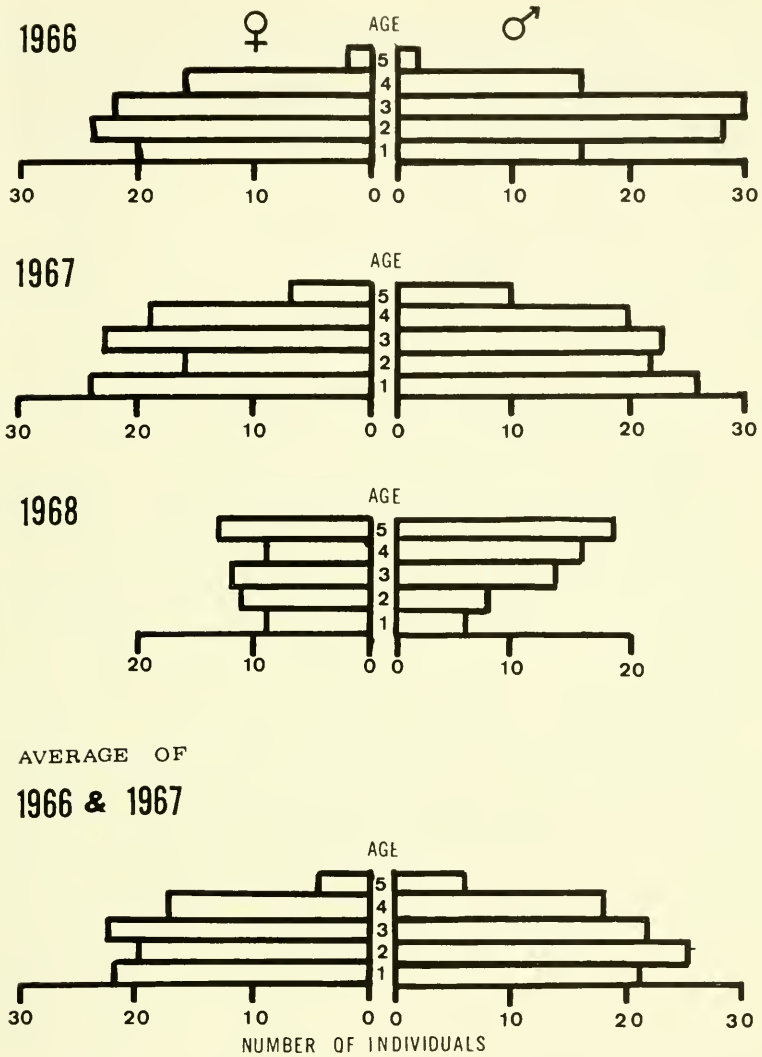

FIG. 10. Population structure calculated from the direct observation of the number of individuals present. Abcissas represent number of individuals.

possibly because the effects of immigration, emigration, and mortality differ in the different age classes.

A second method of determining survivorship relies on the direct observation of mortality within the different age classes and approximates Deevey's (1947) first method. Neither age nor time of death could be observed directly in most instances, but estimates of both are available. The consistency of data obtained from two sources (Tab. 13) encourages confi-

TABLE 13. Observed survivorship in *E. obsoletus*.

Age	Individuals Marked by Fitch (1949) N = 89	Individuals Marked in 1966 (Present Study) N = 78	Individuals Marked in 1967 (Present Study) N = 140*
0-1	0.33	0.27	0.25
1-2	0.36	0.33	0.33
2-3	0.60	0.56	0.47
3-4	0.47	0.42	0.31
4-5	0.33	0.72	0.43
5-6+	0.75	0.67	0.40

* Values for individuals caught in 1967 are somewhat lower than those for the other years because only one year, 1968, was available for their recapture.

dence in their accuracy. The population studied by Fitch in 1949 had already begun a decline which ended in extirpation, yet increased mortality is not indicated.

These records probably have led to an underestimation of survival because it has been impossible to capture all individuals present in each year of the study. To account for the individuals present but not captured in the course of resampling, it is necessary to determine sampling efficiency. In Hayne's (1949b) formula,

$$P = \frac{\Sigma\, w\, X^2}{\Sigma\, w\, X\, Y}$$

P, the population size and X, the total number of individuals marked, estimate sampling efficiency when expressed as the ratio $\Sigma x/P$. Multiplying the number recaptured in the subsequent sample by the reciprocal of sampling efficiency would provide an estimate of the total number that were marked and present. A second method of estimating sampling efficiency has been suggested by H. S. Fitch (pers. comm.) and it seems to eliminate the bias that might result from certain individuals being prone to repeated capture. Animals initially known from capture by hand and those initially trapped are heuristically considered as different populations. Assuming that these two populations are distributed randomly with respect to one another, the percentage of hand-caught animals recaptured by trapping should measure the efficiency of trapping and the percentage of trap-captured animals recaptured by hand should estimate the efficiency of hand capture. The weighted sum of these efficiencies within a season estimates the total sampling efficiency in that season.

Sampling efficiencies derived by Fitch's method are 54.1% for 1967 and 72.0% for 1968. Corresponding weighted averages of efficiencies obtained by Hayne's formula (1967=66.5%, 1968=61.2%) differ from those obtained by Fitch's method, but both methods indicate a similar average sampling effi-

Table 14. Estimation of survivorship using estimates of sampling efficiency.

Year	Age	No. Marked in First Year	No. Recaptured Following Year	Sampling Efficiency	Marked Skinks Present in Second Year	Indicated Survivorship
1966–1967	0-1	11	3	0.37	9	0.82
	1-2	9	3	0.63	5	0.56
	2-3	18	9	0.51	18	1.00
	3-4	19	6	0.62	10	0.53
	4-5	18	7	0.83	8	0.44
	5-6+	3	2	0.83	2	0.67
1967–1968	0-1	4	1	0.48	2	0.50
	1-2	42	14	0.47	29	0.69
	2-3	19	9	0.63	14	0.74
	3-4	37	11	0.52	21	0.57
	4-5	28	12	0.66	18	0.64
	5-6+	10	4	0.66	6	0.60

ciency. Application of Fitch's method to these samples may result in unknown error owing to the spatial and temporal non-randomness noted in the frequencies of capture by hand and capture by trapping.

In both methods estimates of sampling efficiency are affected by immigration, emigration, and unknown mortality, with a resulting error which leads to underestimation. Both tend to overestimate true survival rates and both give surprizingly similar results. For example, estimates of annual crude mortality (which are undoubtedly too low) are: 41.8%, when estimated with Hayne's formula, and 41.0% with Fitch's method. Estimates of age specific survivorship made with Hayne's formula are shown in Table 14.

Two estimates of survivorship rates are now available: (1) observed rates of survivorship (Tab. 13), and (2) rates of survivorship calculated with a measure of sampling efficiency (Tab. 14). The former undoubtedly underestimates survivorship and the latter almost certainly overestimates it. Shown together (Fig. 11 A, B), they possibly bracket the actual survivorship rates.

A third curve (Fig. 11 C), intermediate in value and following the form of the calculated curves, has been derived in part by using the mean of estimates based on the two methods and in part by estimating the number of adults necessary to replace annual losses. Assuming that natality was sufficient to replace losses in 1966 and 1968, about 350 adults are necessary to produce 1000 offspring at the observed rates of reproduction. Thus, curve C represents the patterns of mortality shown by the other estimates of survivorship and the average rate of survivorship necessary for the population to be in equilibrium.

Of possible causes of mortality, evidence on predation (Tab. 15) and on the effect of adverse weather was obtained. Three apparent instances of death by freezing were observed in the field, following frosts in early April in 1967 and 1968 (two instances). Undoubtedly many more such deaths occurred

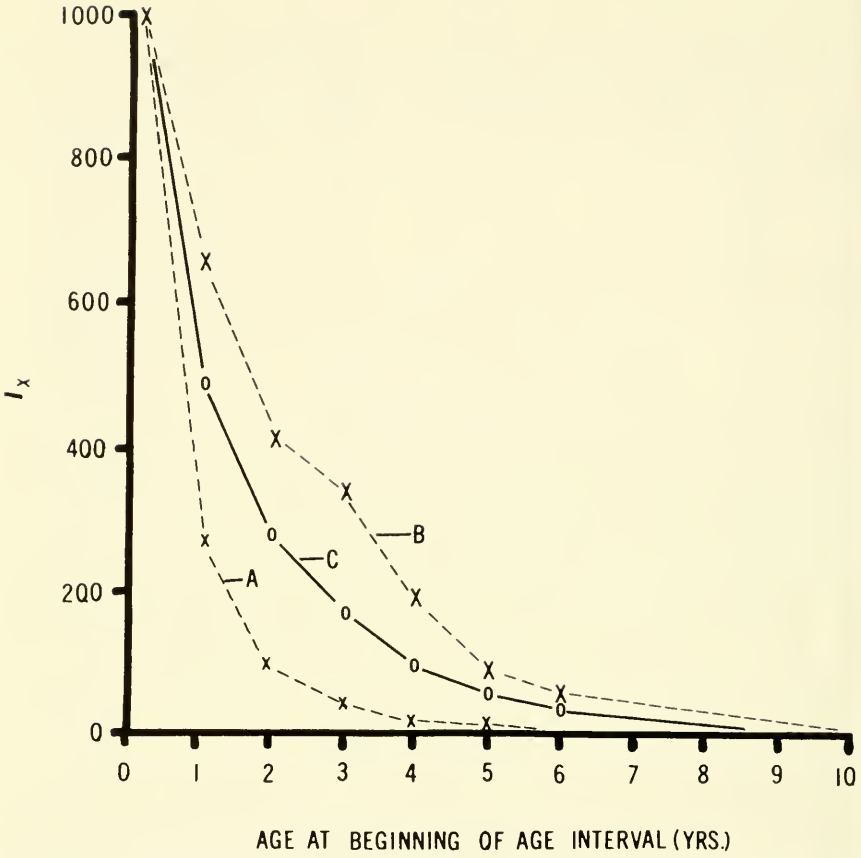

FIG. 11. Survivorship curves for *E. obsoletus*. Curve A is directly observed survivorship. Curve B is an estimate based on collecting efficiency. Curve C is derived, in part, from estimates of reproductivity.

unobserved. It is also probable that many individuals die during hibernation when freezing temperatures penetrate hibernacula. Many marked individuals were caught repeatedly in one season of activity, but failed to appear in the following season, suggesting that they may have died during hibernation.

DISCUSSION

The Great Plains skink exhibits a variety of functional adaptations which favor its survival in the central plains of the United States. These adaptations seem to influence the demography of the species and in turn are influenced by it.

Cycles of activity are closely correlated with environmental temperatures and the resulting cycles of prey availablility. Thus, poikilothermy seems to

Table 15. Predators of *E. obsoletus*.

Predator	Authority
Known Natural Predators	
Blue Racer *(Coluber constrictor)*	Fitch, 1955; present study
Copperhead *(Agkistrodon contortrix)*	Fitch, 1960
Bullsnake *(Pituophis melanoleucus)*	KUNHR, unpublished data
Broad-Winged Hawk *(Buteo platypterus)*	Fitch, 1955
Red-Tailed Hawk *(Buteo jamaicensis)*	KUNHR, unpublished data
Eastern Mole *(Scalopus aquaticus)*	D. R. Clark, pers. comm.
Least Shrew *(Cryptotis parva)*	present study
Predators Having Eaten Captive Skinks	
Prairie Kingsnake *(Lampropeltis calligaster)*	Fitch, 1955
Milksnake *(Lampropeltis triangulum)*	present study
Eastern Massasauga *(Sistrurus catenatus)*	present study
Collared Lizard *(Crotaphytus collaris)*	Burt, 1933
Potential Predators	
Opossum *(Didelphis marsupialis)*	Fitch, 1955; present study
Striped Skunk *(Mephitis mephitis)*	Fitch, 1955; present study
Spotted Skunk *(Spilogale interrupta)*	Fitch, 1955

allow the lizards to be highly efficient predators on insects because they are inactive and conserving energy when their prey species are inactive and unavailable. The annual spring emergence of males somewhat earlier than females may be related to the reproductive cycle and may have a physiological or behavioral basis.

Air temperatures seldom reach the preferred temperature of *E. obsoletus* and individuals must behaviorally raise their temperatures. Unlike many other species of reptiles, these skinks seldom bask in open sunlight; they attain the temperatures necessary for activity in burrows that are excavated beneath exposed rocks. Here, they can reach high temperatures while avoiding the potential dangers of being exposed at temperatures below the normal activity range. The virtual restriction of the species to rocky hillsides is possibly a result of the thermodynamic properties of the rocks which act as reservoirs of thermal energy, available to the skinks throughout most of the daylight hours.

Information indicating that lizards may somehow behaviorally cause their temperatures to rise faster than the substratum (Fig. 6) must be interpreted cautiously. As shown by Heath (1964), a temperature differential between a reptile and its surroundings may be due to the physical properties of the animal and does not necessarily indicate the operation of thermoregulatory mechanisms. However, the skinks may hasten warming by pressing their bodies against the undersurfaces of exposed rocks.

Cowles and Bogert (1944) have described the voluntary minimum as "The low temperature that will cause diurnal animals to become photophobic, or to retreat to their underground shelters . . .". Temperatures of

animals burrowing at the cold end of the gradient (Tab. 4) widely overlap the normal activity range, indicating that the burrowing response alone is not a good criterion for showing the voluntary minimum temperature. Other observations (Tab. 5) tend to support those of Regel (1967) who reported that the preferred temperature range of other species of lizards varies during parts of the daily cycle. He argued that this voluntary hypothermia is advantageous to lizards at night.

The lethal high temperature was not determined in the present study, but Dawson (1960) reported the deaths of some individual *E. obsoletus* exposed to temperatures between 40 and 42°C for four to five hours, and the deaths of all individuals kept above 42°C for that length of time. Thus, like the lethal minimum temperature, the lethal maximum cannot be determined precisely because it is a function of both the intensity and duration of exposure.

Almost from its beginning the concept of home range has been the subject of controversy. Although few now doubt the existence of home range for most species, opinions differ on the proper method for determining the size and degree of utilization of the home range. My understanding of home range is similar to that implied in other studies in lizard ecology (*e.g.*, Tinkle, 1967a,b). The studies of Hayne (1949a), Tinkle, McGregor and Dana (1962), Jorgenson and Tanner (1963), and Tinkle (1967a) are excellent comparisons of different methods of determining home range. Further comparisons based on my data may be instructive because the different methods seem to differ in precision and accuracy and because of the unusual nature of movements in *E. obsoletus*.

Fitch (1955, 1958b) distinguished two types of movements in this species: movements within the home range, and shifts, supposedly from the area of one home range to another. He considered movements over 200 feet to be such shifts while movements in excess of 150 feet have been considered shifts in the present study. In Fitch's study, 19% of all recaptured animals had shifted with an average displacement of 264 feet. In the present study, only 5% of the animals made shifts, and the distances averaged 195 feet. Perhaps the greater frequency of shifts and a larger average home range size calculated by Fitch reflected the generally unfavorable habitat and declining population at the location of his study.

The home range size calculated by the minimum polygon method is strongly related to the number of times individual animals are captured (Tab. 6) and thus the mean size of home range is of little use. One use of this method is in considering a few of the more complete estimates as minimum sizes for comparison with other methods. Mean distance moved probably overestimates the size of home range. Most authors using this method have stressed its value as an indicator of the relative vagility of

species, but have been reluctant to calculate home range sizes directly with it (Hayne, 1949a). The mean maximum distance moved, while seldom used as a measure of vagility, would presumably make these estimates relatively independent of trap density or collecting effort. Probability density function has been advocated by Hayne (1949a) and Dice and Clark (1953), and has been applied to the study of lizards by Jorgenson and Tanner (1963) and Tinkle (1967a). Tinkle (1967a) found that the method provides remarkably constant estimates with different sets of data. He stressed the value of the mean radius of recapture as a comparative statistic, but discouraged calculation of home range sizes from it. Of all methods employed in the present study, mean radius of recapture may be the best indicator of vagility because it shows the least dependence on the number of times individuals were captured (Tab. 9).

The age of breeding maturity in females seems to be individually variable with differences in weather possibly accounting for varying proportions of three year olds noted to be gravid in different years. Breeding maturity is attained late in comparison with other species of lizards. Even lizards of comparable size such as *Crotaphytus collaris* may produce eggs in the first year of life (Fitch, 1956) whereas it takes females of *E. obsoletus* at least three years to reach maturity.

The production of eggs was estimated to average approximately 50% of the reproductive potential for the years of study. However, there was great yearly variation and these variations may result principally from patterns of weather. The hot, dry summer of 1966 and the cool, wet spring of 1967 are thought to have contributed to poor reproductive success in 1967.

E. obsoletus may suffer relatively little mortality from predation. The known predators either eat a wide variety of foods or are mainly restricted to taxonomic groups other than reptiles. The greatest mortality factors may be fire, weather, and other factors acting independently of density.

Most features of the ecology of the species are presumed to be correlated with its survivorship. Characters such as large size, low vagility, temporally restricted activity, and the brooding of eggs appear to increase survivorship. Increased survivorship allows for the maintenance of a low reproductive potential which conserves energy and may also contribute to an even greater rate of survival. Mortality is high in the interval 0-1 years because of the actions of natural selection. The rate tends to decrease in the 1-2 and 2-3 year intervals, but it shows some tendency to increase in the 3-4 and 4-5 year intervals. The initial decrease would be expected because the individuals in a cohort, becoming older, would gain in size and experience. An increase in the mortality rate in the 3-4 and 4-5 year intervals would seem to be related to reproductive activity. Three year old males and four year old females are probably breeding for the first time with the attendant risks which would

probably increase mortality. The Type IV survivorship curve (Slobodkin, 1961) evidenced by most lizard species (and most small vertebrates) is also characteristic of *E. obsoletus*. The species differs from most other lizards in its greater average lifespan (about 1.5 years as extrapolated from Fig. 11C). Among the better-known species of lizards, only the nocturnal, viviparous *Xantusia vigilis* (Zweifel and Lowe, 1966) has comparable survivorship.

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

AN ILLUSTRATED, ANNOTATED CATALOGUE OF AFRICAN MECOPTERA

By

George W. Byers

Vol. XLIX Pages 389-436 Nov. 19, 1971 No. 8

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An Illustrated, Annotated Catalogue of African Mecoptera[1]

George W. Byers

ABSTRACT

For each known species of African Mecoptera, the following are presented: valid name, synonyms, comments on the type(s), geographic and seasonal distribution, review of literature references to the species, and major recognition characters. Lectotypes are designated for seven species of *Bittacus: alluaudi, discors, schoutedeni, sjostedti, testaceus, weelei, zambezinus.* Nine nominal species are placed in synonymy for the first time: *Bittacus jeanneli* Navás and *B. zavattarii* Capra = *B. alluaudi* Navás, *B. rhombicus* Kimmins = *B. berlandi* Capra, *B. patrizii* Navás = *B. discors* Navás, *B. similis* Kimmins = *B. lineatus* Navás, *B. lestagei* Kimmins = *B. schoutedeni* Esben-Petersen, *B. brincki* Tjeder = *B. testaceus* Klug, *B. longistigma* Navás and *B. wittei* Navás = *B. weelei* Esben-Petersen.

INTRODUCTION

Somewhat fewer than half the species of Mecoptera now known from Africa were included in Esben-Petersen's (1921) monographic revision of the order. These comprised the few species described very early by Thunberg (1784) and Klug (1838) and several named in the first 20 years of this century by Weele and Navás, and by Esben-Petersen himself. Lestage (1929) briefly reviewed the African fauna, including 25 species, most of which he had not seen, and illustrating only one of them. Wood (1933) described three new species and discussed eight others, all from South Africa. The most recent major work on African Mecoptera was that by Tjeder (1956) on 18 South African species, of which he described five as new.

Tjeder's descriptions and illustrations treat two-thirds of these South African species in detail, but he had not seen examples of the others. Many of the species from central Africa have been only briefly described and scarcely adequately illustrated, if at all. It is therefore my purpose here to list

[1] Contribution no. 1468 from the Department of Entomology, The University of Kansas, Lawrence, Kansas 66044, U.S.A.

all the species so far described from Africa and, on the basis of a study of the type specimens of many of them (particularly those from outside South Africa), to draw attention to certain taxonomically important structural details, to illustrate the types, and to comment on probable synonymy.

Each species entry consists of (1) the valid species name, its author, and reference to the original description, (2) synonyms, if any, with author and reference, (3) summary data for the type(s) of the valid species (sex, label information, and repository), (4) summary of known range and seasonal distribution, (5) brief review of literature references to the species, (6) comments on the type specimen(s) and on the similarity of the species to others, particularly with reference to synonymy, including brief mention of structural characters useful in recognition of the species.

The illustrations in this catalogue are admittedly greatly stylized but were made primarily to draw attention to the general shapes of the structures represented. They are fairly accurate with respect to outline and scale, having been drawn with the aid of a camera lucida. The epiandrial lobes of the ninth abdominal tergum of the male have been arbitrarily shaded differently from other structures partly because they often are somewhat paler than other sclerotized parts but mainly to emphasize their shape. Since the drawings are of the actual types or other particular specimens, the subjects are not uniformly positioned.

ACKNOWLEDGMENTS AND SOURCES

This work has been generously supported by Grant GB-7045X from the National Science Foundation, which support provided for visits to most major European museums for the study of type specimens.

The institutional collections containing type specimens and others mentioned hereinafter are abbreviated, if referred to repeatedly, according to the following alphabetical list. I wish to thank the entomologists whose names appear after the name of their museum for their kind assistance during my visits or at other times, through correspondence. The collections of the South African museums were not seen, but the types involved have all been carefully described and well illustrated by other authors.

Barcelona—Museo de Ciencias Naturales, Barcelona, Spain; Dr. F. Español.

Berlin—Museum für Naturkunde (formerly Zoologisches Museum) der Humboldt Universität, Berlin, DDR; Dr. W. Crome and Dr. H. Wendt.

BMNH—British Museum (Natural History), London, England; Mr. D. E. Kimmins.

Brussels—Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; Dr. M. A. Collart and Dr. G. Demoulin.

Deutsches Entomologisches Institut, Eberswalde bei Berlin (formerly Berlin-Friedrichshagen), DDR; Dr. G. Friese.

Durban—Durban Museum and Art Gallery, Durban, Natal, Republic of South Africa.

Genova—Museo Civico di Storia Naturale Giacomo Doria, Genova, Italy; Dr. Delfa Guiglia.

Lund—Zoological Institute, University of Lund, Lund, Sweden; Dr. Bo Tjeder.
Paris—Museum National d'Histoire Naturelle, Paris, France; Dr. Simone Kelner-Pillault.
Pretoria—Transvaal Museum, Pretoria, Transvaal, Republic of South Africa.
SAM—South African Museum, Cape Town, Cape Province, Republic of South Africa.
Stockholm—Naturhistoriska Riksmuseet, Stockholm, Sweden; Dr. P. I. Persson.
Tervuren—Musée Royal de l'Afrique Centrale, Tervuren, Belgium; Dr. P. Basilewsky.
Universitetets Zoologiske Museum, Copenhagen, Denmark; Dr. Børge Pedersen.
Wien—Naturhistorisches Museum, Wien, Austria; Dr. A. Kaltenbach.

I wish particularly to thank Dr. C. N. Smithers, of the Australian Museum, Sydney, for reading the manuscript and offering suggestions, Mr. J. G. H. Londt, of Rhodes University, Grahamstown, South Africa, for stimulating correspondence that led to the preparation of this paper, and Dr. Charles R. Wyttenbach, for his careful editing and many useful suggestions.

ABBREVIATIONS

In the following species accounts, the nomenclature of wing veins follows the Comstock-Needham system. A few additional abbreviations are used for venational characters that have been found especially useful in taxonomy of Mecoptera:

Av—apical cross-vein between Cu_2 and 1A near the distal end of 1A.
Pcv—pterostigmal cross-vein(s): short cross-veins between R_1 and R_2 at posterior margin of stigma.
Scv—subcostal cross-vein: short cross-vein between distal half of Sc and R_1.
FRs—first fork of radial sector (Rs), separation of R_{2+3} from R_{4+5}.
ORs—origin of radial sector (Rs) from R_1.

In reference to figures, the abbreviations ♂ gen. and ♀ gen. pertain to male and female genitalia, or, more correctly, the terminal abdominal segments.

DISTRIBUTION AND TAXONOMY

Of the nine families of extant Mecoptera, only the Bittacidae are known from Africa. This family has numerous genera in the New World, particularly in South and Central America, but only two occur in Africa: the monotypic *Anomalobittacus,* and *Bittacus,* which is widespread also in Europe, Asia, and North and South America. *Anomalobittacus* appears to be restricted to southernmost Africa, while the many species of *Bittacus* range northward, in non-desert areas, from the Cape to the Sahara.

Only the most generalized geographic patterns are evident from the distributions now known because our knowledge of the ranges of most species is based upon small, often widely scattered samples or even unique individuals. These samples give the impression of rather limited ranges for most of the species. *Bittacus chevalieri, montanus* and *weelei* are exceptions; some other ranges described as extensive turn out to be based on records of more than one species.

Differentiation of species in the genus *Bittacus* has usually been based on external reproductive structures of the male, and upon certain aspects of wing venation and coloration of body and wings. Dr. Bo Tjeder has found several primarily genitalial characters of the females taxonomically useful and reliable by reason of their constancy within a species but variability from one species to another. Many of the problems existing in the taxonomy of African Bittacidae stem from the past practice of naming new species from females without sufficiently differentiating them from closely similar forms. Perhaps utilization of Tjeder's methods will serve to clarify some of these problems. In my own work on African species, however, I have not dissected any of these female holotypes.

Various authors (e.g., Lestage, 1917; Tjeder, 1956; Londt, 1970) have shown that venation in African bittacids is in many instances unstable, particularly in the apical one-third of the wings. As far as I am aware, however, no similar examination has been made of intraspecific variation in the other characters, such as male genital appendages, so much relied on in taxonomy. As a result, we do not know how reliable some of these characters really are. Most of the variation that has been described in the differentiation of species is real enough, but much, it seems to me, has depended on how the specimen was preserved (which may affect the apparent shape of a sclerite by folding or warping), whether sclerites were distended or contracted (e.g., the positions and apparent lengths of cerci and proctiger in relation to the other structures of the genital segment), or the age of the individual when preserved (as this affects color or degree of sclerotization).

My interpretation of variation in the African Bittacidae has been strongly influenced by my experience with variation in the few (only seven) but widespread species of *Bittacus* in eastern North America. In studying the North American fauna, one becomes accustomed to working with hundreds of individuals of most species and thereby begins to get a "feel" for the extent of variation within one species, either at one locality or throughout the species' range, and from one season to another. Accordingly, where I have in the following catalogue stated an opinion on synonymy, this is not because I do not appreciate the differences between two holotypes but merely because I make a different evaluation of these differences from that made by earlier taxonomists. In some cases, where it seems to me unlikely that earlier taxonomists were able to compare types of synonymous species, I have illustrated both or all the type specimens involved, at the risk of being accused of wasting valuable space. In the absence of very convincing evidence of synonymy, I have retained separate species names for very similar forms, pending possible clarification through further collecting or more detailed examination of the types.

SYSTEMATIC CATALOGUE

Anomalobittacus Kimmins

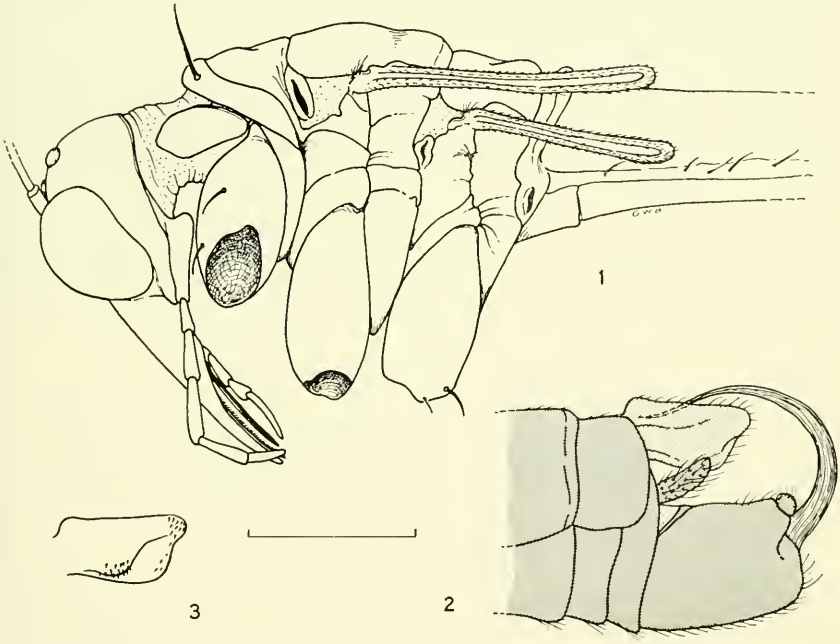
Anomalobittacus gracilipes Kimmins

Anomalobittacus gracilipes Kimmins 1928: 396, unnumbered figure (♂ gen.).

Type: ♂ holotype, Cape Town, South Africa, 18 November 1915, K. H. Barnard; BMNH.

Range: Apparently restricted to southwestern Cape Province, Republic of South Africa.

Both Kimmins (1928) and Wood (1933) illustrated the genitalia of the male but not the thorax, which is easily the most interesting thing about the species. Consolidation of the thorax is seen mainly in the expansion of the nota and reduction of the pleural sclerites, especially of the prothorax, and the broad fusion of these with the nota (Fig. 1). The degree of consolidation is only slightly less than in *Apterobittacus apterus* (MacLachlan) of western North America. Wood (1933) described the female (as "allotype") and redescribed the male (from two ♂ "paratypes"), correcting some minor errors in the original description. Tjeder (1956) mentioned this species but had seen no specimens of it.



Figs. 1-3. *Anomalobittacus gracilipes,* male. **1,** head and thorax, left lateral aspect (legs removed beyond coxae); **2,** terminal abdominal segments, left lateral aspect; **3,** right epiandrial lobe, mesal aspect. Scale line 1 mm.

The epiandrial lobes of a male from DuToits Kloof, Cape Province, 22 November 1949 (Figs. 2-3) bear 11-12 spines on their inner surface near apex, a dozen or so more on a thick lobe near the lower margin, and a few near the posterior margin. This differs somewhat from the arrangement illustrated by Wood. Wood's description of the female does not mention the many long, stout black bristles on the subgenital plates.

Bittacus Latreille

Except for the one species of *Anomalobittacus* above, all African species of Mecoptera belong to this genus. Tjeder (1956: 347-348) gave a good summary of the taxonomically useful structures and established some species groups.

Bittacus aequalis Navás

Bittacus aequalis Navás 1914a: 47, fig. 22 (♂ gen.).

Type: ♂ holotype, "Landjoro, dans le Pori de Sérenghéti," British East Africa (Kenya), 900 m, March 1912, Alluaud and Jeannel; Paris.

Range: Type locality only; this is Lanjoro Ndoyo, 3°26′S, 37°46′E, on the Serengeti Plain east of Mt. Kilimanjaro and a little southeast of Taveta, southern Kenya (the region not to be confused with the better known Serengeti Plain west of Kilimanjaro in northern Tanzania).

This is a distinctive species, briefly described and badly illustrated by Navás. Esben-Petersen (1921) merely repeated the description, and Lestage (1929) listed the species and included it in a key. Besides the type, there are 2 ♂, 1 ♀ of *aequalis* in the Paris Museum, but I know of no other specimens.

The epiandrial lobes (Figs. 4-6) have an unusually long ventral process, an apical brush of long hairs, and a scattering of small denticles on the upper, inner surface near the tip. Venation: no Av, Scv opposite or slightly beyond FRs, two Pcv. *B. aequalis* seems to me close to but different from males identified by Navás as *B. chevalieri* Navás (which see).

Bittacus africanus Esben-Petersen

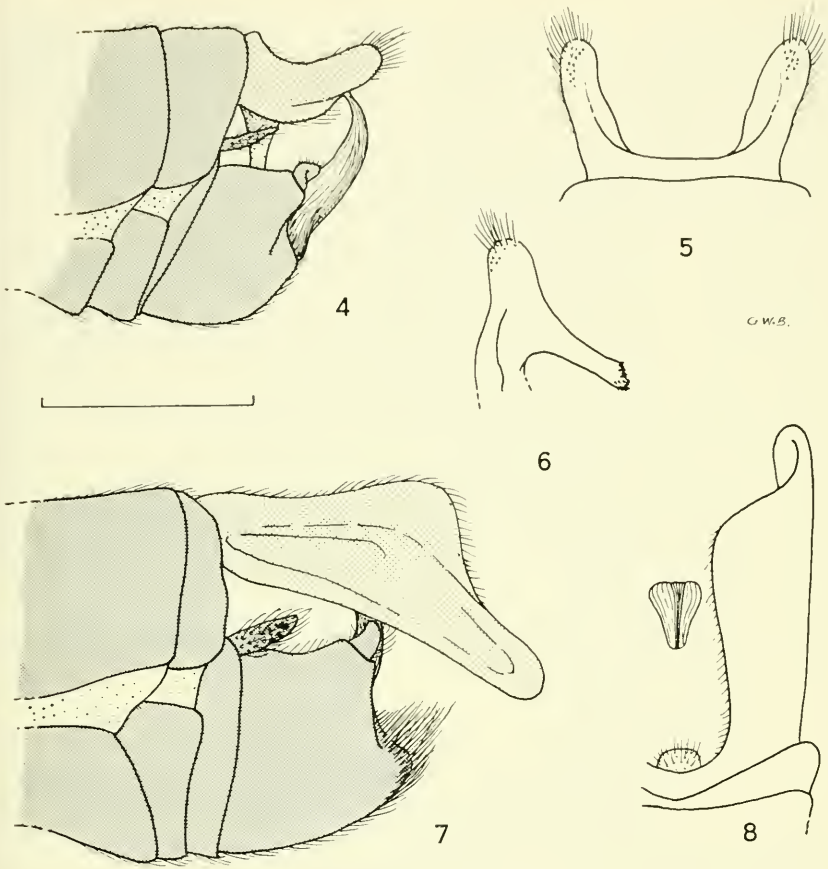
Bittacus africanus Esben-Petersen 1915: 235-236 (no figs.).

Type: ♂ holotype, Beni, eastern Congo, October 1910, Grauer; Wien.

Range: Type locality only; this is primeval forest ("Urwald") near Beni, 0°30′N, 29°28′E, west of the Ruwenzori Mountains and north of Lake Edward, eastern Democratic Republic of the Congo.

Esben-Petersen (1921) summarized the original description and illustrated the terminal segments of the holotype (his fig. 142). Lestage (1929) merely listed the species and reviewed its characters in a key. I know of no specimens of *africanus* other than the holotype. It seems quite a distinct species.

There are no blackened spines and no processes on the inner surfaces of



Figs. **4-6.** *Bittacus aequalis,* male holotype. **4,** terminal abdominal segments, left lateral aspect; **5,** epiandrium, dorsal aspect; **6,** right epiandrial lobe, dorsomesal aspect. Figs. **7-8.** *Bittacus africanus,* male holotype. **7,** terminal abdominal segments, left lateral aspect; **8,** left epiandrial lobe and parts of aedeagus and proctiger, dorsal aspect. Scale line 1 mm.

the epiandrial lobes (Fig. 7). The proctiger is small, almost wholly concealed beneath the ninth tergum, in dorsal aspect (Fig. 8). Venation: Av present, Scv before FRs, two Pcv, and two cross-veins between R_2 and R_3. The dististyles are unusually long for a *Bittacus*. Aedeagus short, simply curved, not coiled (Fig. 8).

Bittacus alluaudi Navás

Bittacus alluaudi Navás 1914a: 45, fig. 20 (♂ gen.).
B. jeanneli Navás 1914a: 46-47, fig. 21 (♂ gen.). New synonymy.
B. zavattarii Capra 1939: 165-169, figs. 4 (wing), 5 (♂ gen.). New synonymy.

Type (of *alluaudi*): ♂ syntype, Taveta, British East Africa (Kenya),

750 m, March 1912, Alluaud and Jeannel; Paris. This specimen is hereby designated lectotype. One supposes, from the fact that Navás listed three localities for the species, that there were initially at least three syntypes. The Paris Museum also has 1 ♂ and 1 broken specimen of *alluaudi,* but these do not bear type labels. Only the male was described.

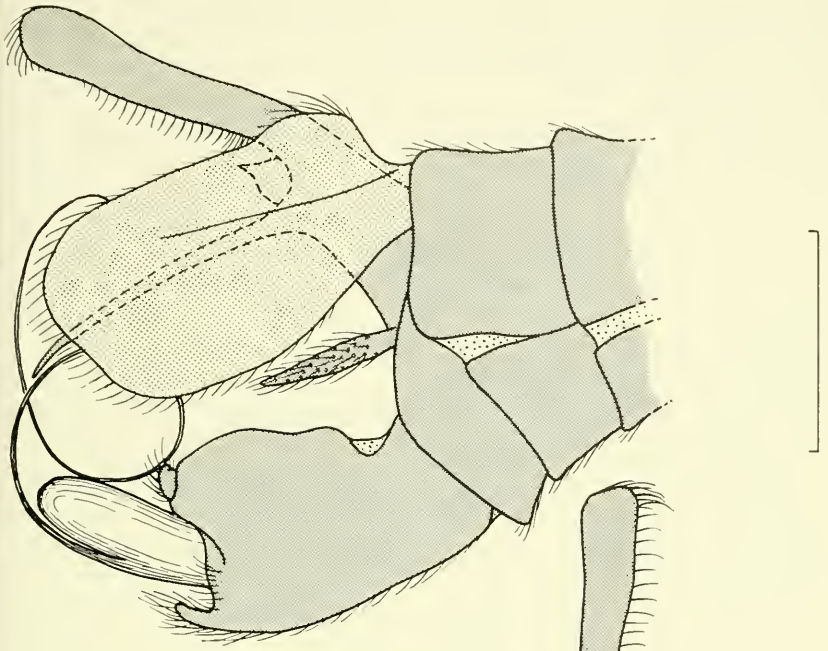
Range: Kenya and adjacent northern Tanzania (Tanganyika) and southern Ethiopia; March-April. Taveta is at 3°24′S, 37°41′E, southeast of Mt. Kilimanjaro.

Esben-Petersen (1921) repeated the original descriptions of both *alluaudi* and *jeanneli* but had not seen either. Both he and Lestage (1929) commented briefly on the remarkable terminal segments of *alluaudi,* but Lestage otherwise only listed the species.

This species is characterized by two striking structural specializations, the conspicuous proctiger and the large penunci beside the base of the aedeagus (Fig. 9). The dorsal prolongation of the proctiger is compressed, at first appears blade-like, but actually comprises two laminae joined dorsally for their entire length; the lower prolongation is long and acuminate. Conspicuously developed penunci are correlated with an unusually large and complicated proctiger also in *Bittacus fumosus* (which may prove to be conspecific with *alluaudi*), in the southern African species *B. zambezinus* Navás and *B. natalensis* Wood, and in several species of *Bittacus* in eastern Asia and North America.

Navás differentiated *jeanneli* from *alluaudi* on the basis of differences in the shape of the epiandrial lobes, minor differences in the ninth abdominal sternum, overall size and paler color. The holotype of *jeanneli* is in the Paris Museum, permitting side-by-side comparison of it with *alluaudi.* The differences described by Navás are real, but I regard them as falling within the probable range of intraspecific variation. The type of *jeanneli,* a small, somewhat teneral individual, was collected at the same time and place as that of *alluaudi* and has virtually the same structure in every detail.

The male holotype and one female paratype of *B. zavattarii* were taken near the border town of Moyale, southernmost Ethiopia (3°34′N, 39°04′E), on 15 April 1937. (The main city of Moyale is in Kenya.) Capra (1939) recognized the close similarity of *zavattarii* (Fig. 10) to *alluaudi* but observed that the epiandrial lobes in the latter were more regular in outline, with straight dorsal margin and more convex posteroventral angle. He also noted slight differences in wing shape between the two and minor differences in venation, which he regarded as probably without diagnostic significance. Capra also realized that *B. jeanneli* Navás and the so-called male type of *B. fumosus* E.-P. differed only slightly from his *zavattarii.* Capra in fact made a far more accurate, detailed study of the African Mecoptera within the scope of his paper than anyone before his time had done, and he set the pattern



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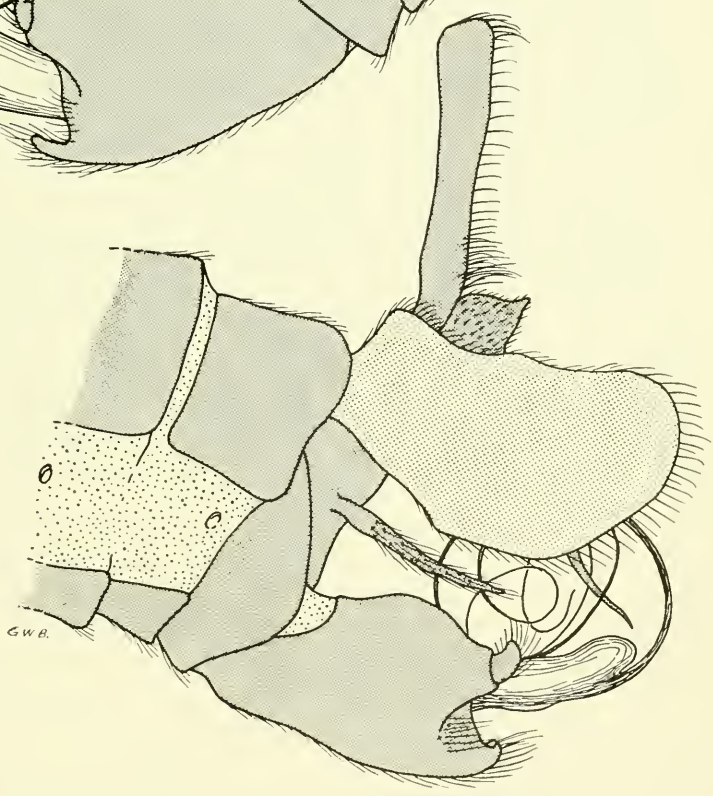

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Fig. 9. *Bittacus alluaudi,* male holotype; terminal abdominal segments, right lateral aspect.
Fig. 10. *Bittacus zavattarii,* male holotype; terminal abdominal segments, left lateral aspect.
Scale line 1 mm.

for the later works of Wood, Tjeder and Smithers. Yet, although I appreciate the superiority of his work, I have reached a different taxonomic evaluation of it and therefore relegate *zavattarii* to the synonymy of *alluaudi*.

There is, in the BMNH, a male from the vicinity of Kitui, Kenya, identified by Esben-Petersen as *Bittacus fumosus*. It is the only male that has been associated with that name, which may explain why it bears a label stating it is a "type" (although *fumosus* was described on the basis of one specimen lacking the terminal abdominal segments). This male (Figs. 21-23) closely resembles *alluaudi* in structure of genital appendages, proctiger, etc., except that its proctiger and ninth sternum have apparently been pushed downward in the process of preservation. The Scv in this male is slightly beyond FRs, as in the holotype of *fumosus*, but it is before the FRs in the type specimens of *alluaudi, jeanneli* and *zavattarii*. Since the position of the Scv in relation to the FRs is ordinarily constant within a species, I tentatively accept the Kitui male as conspecific with the holotype of *fumosus* and distinct from *alluaudi*. If, however, further study of the male terminalia indicates the Kitui male is conspecific with *alluaudi, jeanneli* and *zavattarii* in spite of this venational difference (and if it is still accepted as actually *fumosus*), all these species will fall into the synonymy of *fumosus* Esben-Petersen 1913.

Bittacus angulosus Tjeder

Bittacus angulosus Tjeder 1956: 378-381, figs. 93 (wings), 94-98 (♀ gen.).

Type: ♀ holotype, Krantz Kloof Nature Reserve, elev. 2000 ft, 12-15 miles inland from Durban, Natal, 10 May 1915, H. W. Bell-Marley; Durban.

Range: Type locality only, vicinity of Durban, Natal, Republic of South Africa.

Known from the holotype and one male, this species is very similar to *B. walkeri*. The shape and color of the wings and their venation are the most conspicuous similarities between the two nominal species. There are distinct differences between the female assigned by Tjeder to *walkeri* and the holotype of *angulosus*, such as abdominal shape, sclerotization of acrotergites, and setal armature of the subgenital plate.

The male judged conspecific with the type of *angulosus* was included by Esben-Petersen (1917, fig. 4, and 1921) and Wood (1933, fig. 12) in *B. walkeri* Esben-Petersen. (Compare *angulosus* with *kimminsi* and *walkeri*, which three comprise a species group.)

Bittacus armatus Tjeder

Bittacus armatus Tjeder 1956: 360-362, figs. 34-35 (wings), 36-41 (♂ gen.), 42-46 (♀ gen.).

Type: ♂ holotype, Minastune, Transvaal, 1-2 January 1921; Pretoria.

Range: Transvaal (Minastune, Barberton, Waterval Onder), Southern Rhodesia (Hope Fountain); November-January.

In the original description of *armatus,* Tjeder (1956) compared it with *testaceus* (as *brincki*), noting the shorter, wider epiandrial lobes in *armatus,* the four blackened denticles on the inner surface of the apex of each lobe, and other details of structure and color.

Smithers (1959), in a key, compared *armatus* with other species occurring in Southern Rhodesia.

Bittacus berlandi Capra

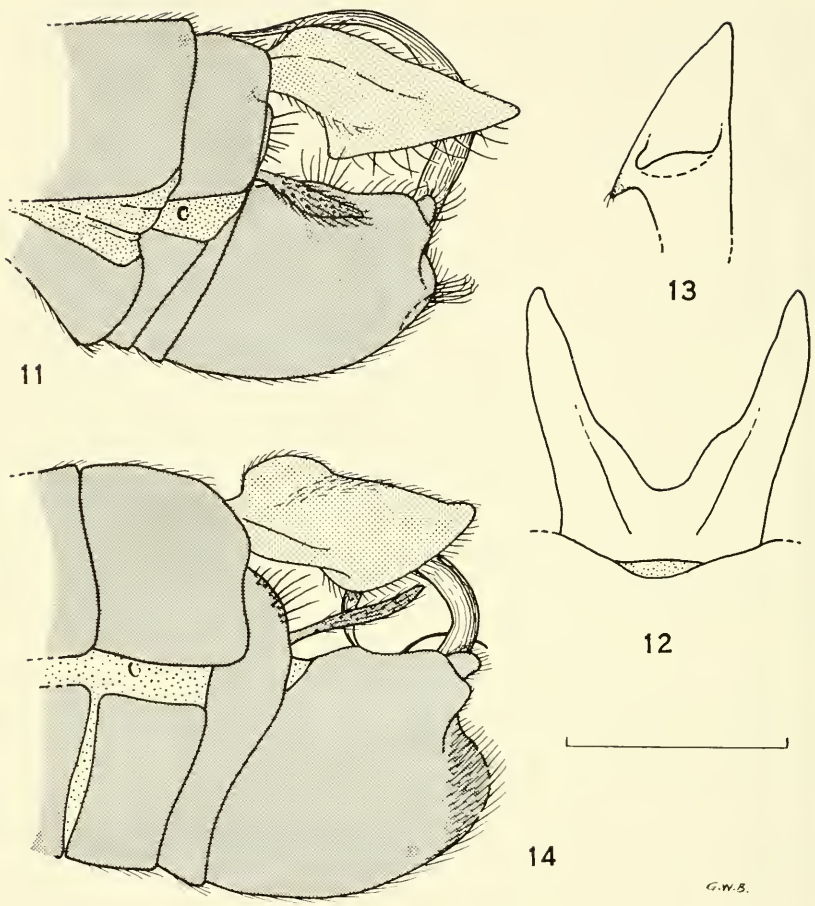
Bittacus berlandi Capra 1939: 175-177, figs. 9 (wings), 10 (♂ gen.).
B. rhombicus Kimmins 1957: 38-39, figs. 6-7 (♂ gen.). New synonymy.

Type (of *berlandi*): ♂ holotype, "Afrique or. allemande, Kilimandjaro, versant sud-est, zone inferieure, Neu-Moschi," 800 m, April 1912, station 72, Alluaud and Jeannel; Paris. For more than 30 years after its description this specimen, bearing no type label, stood in the Paris Museum under the name *sjostedti* (although Capra had attached to it a label reading "*Bittacus* sp. prope *Lachlani* Nav., certe non *Sjöstedti* Weele. . . ."). Capra's published photograph of the wings, showing peculiar spur-like veins extending from Cu_1 approximately opposite the Av, in all four wings, makes possible the positive identification of this male as the holotype; accordingly, I have so labelled it.

Range: Vicinity of Moshi (3°20′S, 37°20′E), northern Tanzania (Tanganyika), southeast of Mt. Kilimanjaro; Nziu (1°49′S, 37°32′E), Unoa District, Kenya; April, December.

This species has not been mentioned by any authors since 1939. Kimmins (1957) compared his species *rhombicus* with *sjostedti* and *peterseni,* but its holotype (in the BMNH) agrees in detail with *berlandi,* and its type locality is less than 100 miles north of Kilimanjaro. This is also the species identified as *sjostedti* by Navás (1914a: 44). To what is known about the species from these two holotypes, I can add only that there is in the Paris Museum one additional male collected at the same place and date as the type of *berlandi.*

Although *berlandi* rather closely resembles both *boranicus* Capra and *sjostedti* Weele, it seems to me distinct. The epiandrial lobes (Figs. 11-13) are acute at the apex, divergent, their mesal surfaces without spines but with a darkened, subconical, ventral projection and a shallow pocket near mid-length. The proctiger is small and close beneath terga 8 and 9. Venation: Av present, Scv before FRs, two Pcv (three in type of *rhombicus*). The venation in the holotype of *berlandi* is aberrant; in addition to the small spur veins mentioned earlier, there are other minor deformations, but the extra rank of cells in the discal area (e.g., 4 cross-veins between M_1 and M_2, 5 between M_2 and M_3, etc.) appears to be characteristic of the species.



FIGS. **11-13.** *Bittacus berlandi,* male holotype. **11,** terminal abdominal segments, left lateral aspect; **12,** epiandrium, dorsal aspect; **13,** left epiandrial lobe, mesal aspect. FIG. **14.** *Bittacus boranicus,* male holotype; terminal abdominal segments, left lateral aspect. Scale line 1 mm.

Bittacus boranicus Capra

Bittacus boranicus Capra 1939: 169-171, figs. 4 (wings), 6 (♂ gen., tarsus).

Type: ♂ holotype, "Javello, nei Borana, A. O. I." (Ethiopia), 15-30 May 1937, E. Zavattari; Genova.

Range: Type locality only, in southern Ethiopia. Javello appears on most maps as Yaballo or Yabelo, in the central part of Sidamo Borama, 4°57′N, 38°08′E.

This species remains known from the holotype only (Fig. 14). Capra (1939) compared it with *B. sjostedti, lachlani, oreinus* and *berlandi.* In my

opinion, there is a possibility that *boranicus* is conspecific with *lachlani* and that *berlandi* may not be specifically different from these, despite venational and other minor differences pointed out by Capra.

The apex of the abdomen has been dissected off, cleared and mounted in balsam between slips of glass attached to a pin separate from that carrying the rest of the specimen. The left wings are mounted on a slide preserved together with the specimen. Venation: Av present, Scv before FRs, two Pcv.

Bittacus brincki Tjeder

See *B. testaceus* Klug.

Bittacus burgeoni Navás

Bittacus burgeoni Navás 1930: 312-313, fig. 28 (wing).

Type: ♀ holotype, Haut-Uele, Moto, Belgian Congo, 1923, L. Burgeon; Tervuren.

Range: Type locality only: upper Uele River, northeastern Democratic Republic of the Congo. Moto is at 2°54′N, 29°27′E.

The holotype is badly damaged (and was at the time of description), having no legs, only part of one antenna, the thorax largely eaten by dermestids, the abdomen also partly missing but all segments represented. To me, its most striking characteristic is the acute apex of the wings. In this respect, *burgeoni* resembles *pobeguini* and *kongoloensis,* yet its venation and golden-brown wing color are quite different. I therefore suppose *burgeoni* is a distinct species of which we still do not know the male. Venation: Av present, two Pcv, Scv before FRs, and an extra rank of cross-veins, thus also of cells, in the discal area (3 cross-veins between R_2 and R_3, 4 between M_1 and M_2, 5 between R_4 and R_5 and between R_5 and M_1).

Navás thought *burgeoni* was similar to his species *elisabethae,* which is also from the Congo and is of about the same size, to judge from the types (front wings of both about 19.5 mm). However, in *elisabethae* the wing tip is rounded, the wing color much less intense, and the number of cross-veins in the discal area fewer than in most species of *Bittacus.*

Bittacus capensis (Thunberg)

Bittacus capensis (Thunberg) 1784: 67, fig. 78 (entire insect) (described as *Panorpa*).

Type: ♀ holotype, "Capite bonae spei," (no date); Thunberg collection, Museum of Uppsala University, Uppsala, Sweden. Type locality restricted to Algoa Bay region of southeastern Cape Province by Tjeder (1956: 349).

Range: Eastern Cape Province, Republic of South Africa; September-October.

Two photographs and a series of drawings accompany the account of

capensis by Tjeder (1956) and give a clear impression of the species as represented by the female holotype. Esben-Petersen (1921, fig. 151) illustrated the genitalia of the male accepted as being of this species, and he was followed in this by Wood (1933, fig. 13). Londt has recently (1970, figs. 12-15) illustrated the genitalia of both sexes, redescribed the species and compared it with his new species, *tjederi*. Klug, in 1838, transferred *capensis* from *Panorpa* to *Bittacus*. Walker (1853) and Navás (1909) listed specimens from South Africa, but that listed by Walker is now the type of *Bittacus walkeri* Esben-Petersen. Banks (1913) and Esben-Petersen (1913) discussed the venation and included *capensis* in their keys. Esben-Petersen (1915) and Lestage (1917, 1929) also briefly included *capensis*.

Tjeder (1956) regarded *capensis* as "certainly very scarce," but Mr. J. G. H. Londt has in recent years collected numerous specimens of both sexes of it near Port Elizabeth (see Londt, 1970).

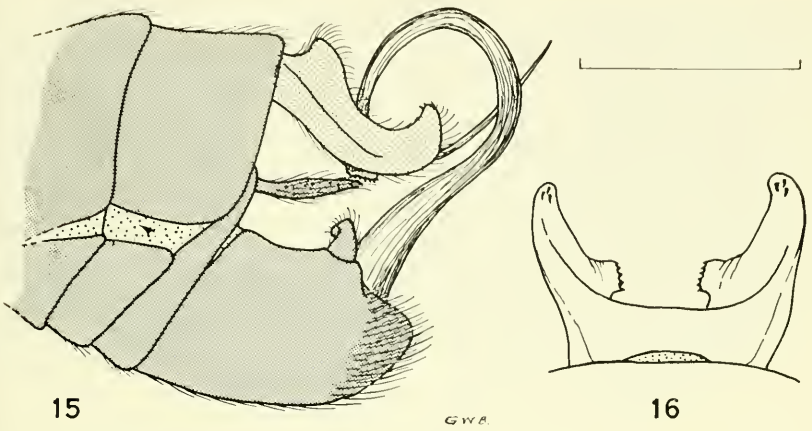
Bittacus chevalieri (Navás)

Bittacus chevalieri (Navás) 1908: 414 (p. 16 in reprinted paper), fig. 17 (wing) (described as *Haplodictyus*).

Type: ♀ holotype, "Africa central, Kanem," 1904, A. Chevalier; Paris.

Range: Soudan (Chad; Mali near 15°N), Senegal; also reported from French Somaliland; September. The type locality is the Kanem region of Chad, approximately 100 miles northeast of the eastern end of Lake Chad.

In 1921, Navás described a male from Senegal (along the Senegal River, between Matam and Bakel, possibly at Dialla, 26 September 1907) as belonging to this species. He also identified as *chevalieri* a male from Nioro, French Soudan (now in western Mali, about 15°15′N, 9°30′W). As there is nothing particularly diagnostic about the female holotype, I have illustrated the male from Nioro (Figs. 15-16), which is also in the Paris Museum and which agrees with the specimen from Senegal and in comparable details with the holotype. I have recently seen one additional male of the form illustrated, from Linguere, Senegal, September 1967, Mission IFAN-Museum, collected by Descarpentries, Leye and Villiers, in the Paris Museum. Although 1900 miles separate northeastern Senegal and Kanem, and Nioro is some 1600 miles west of Kanem, I am tentatively accepting that these males and the female holotype are conspecific. Fraser (1953) reported as *chevalieri* a female from Dogo (= Macina, 13°59′N, 5°20′W), French Soudan (Mali). Navás (1909) recorded *chevalieri* from Obok (= Obock, French Somaliland), some 1800 miles to the east from Kanem. While this is near the same latitude as northeastern Senegal and Nioro and Kanem, I am inclined to doubt that the specimen from Obok is *chevalieri*, an opinion shared by Lestage (1929), who discussed the species at length and who also erroneously stated that the type was a male. I would also question whether the female illustrated by



Figs. **15-16.** *Bittacus chevalieri,* male from Nioro, Mali. **15,** terminal abdominal segments, left lateral aspect; **16,** epiandrium, dorsal aspect. Scale line 1 mm.

Esben-Petersen (1913, fig. 3; 1921, fig. 156) represents the same species as the type of *chevalieri.* Esben-Petersen (1915) listed the species, and Lestage (1917) included it in a key.

In structure of the terminal abdominal segments, the males assigned to *chevalieri* resemble rather closely but differ from the holotype of *B. aequalis* Navás. Venation of these males and of the holotype female: no Av, Scv beyond FRs, one Pcv. See also *B. pobeguini.*

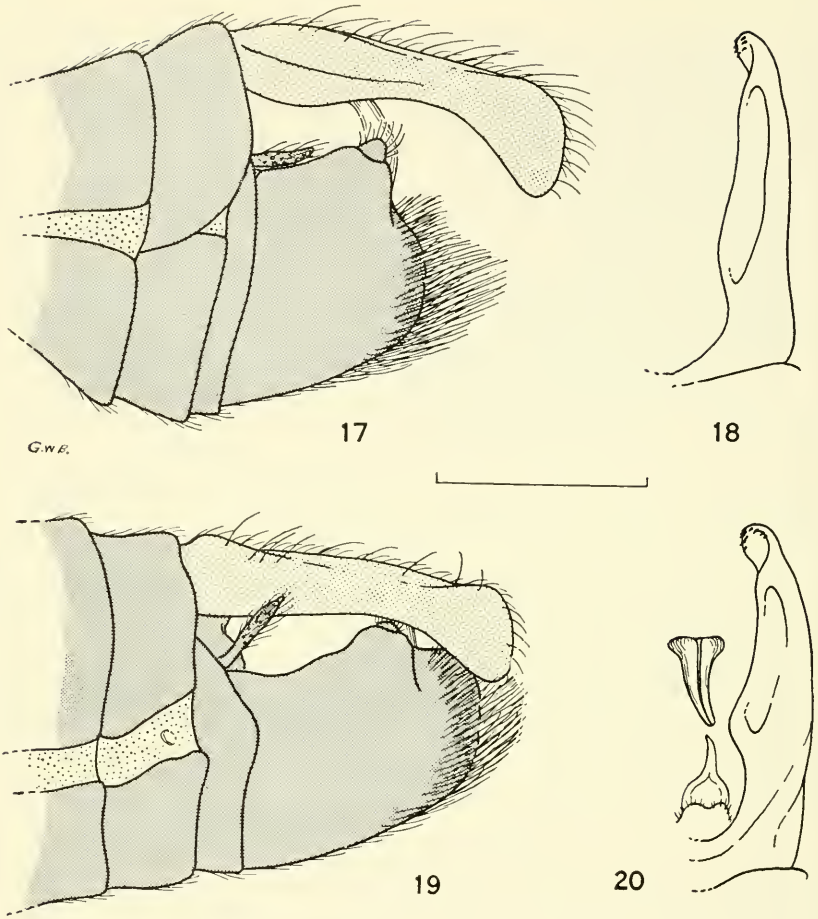
Bittacus discors Navás

Bittacus discors Navás 1914a: 47-48, figs. 23a (♂ gen.), 23b (wing).
B. patrizii Navás 1929: 387, figs. 19a (♂ gen.), 19b (wing). New synonymy.

Types: 1 ♂, 1 ♀ syntypes, "Tavéta, Afrique Orient. Anglaise" (Kenya), 750 m, sta. 65, March 1912, Alluaud and Jeannel; Paris. The male is hereby designated lectotype.

Range: Southern Kenya to southern Somalia. Taveta is at 3°24′S, 37°41′E, southeast of Mt. Kilimanjaro. Cuban Cubú, the type locality of *patrizii,* does not appear in any gazetteers known to me, but Dr. Delfa Guiglia of the Genova Museum has informed me that in August 1923, when he collected the type specimen, Dr. Patrizi was in Basso Giuba (lower Juba River), about 42°35′E and near the equator. Collection dates (March, August) suggest there are possibly two generations a year.

Esben-Petersen (1921) merely repeated Navás' description of *discors,* and Lestage (1929) complained of the uselessness of Navás' description and illustrations but nevertheless attempted to incorporate *discors* in a key. I have found no further mention of either *discors* or *patrizii* since 1929.



FIGS. **17-18.** *Bittacus discors,* male lectotype. **17,** terminal abdominal segments, left lateral aspect; **18,** left epiandrial lobe, dorsal aspect. FIGS. **19-20.** *Bittacus patrizii,* male holotype. **19,** terminal abdominal segments, left lateral aspect; **20,** left epiandrial lobe and parts of aedeagus and proctiger, dorsal aspect. Scale line 1 mm.

Two aspects of the genitalial structure of *discors* (Fig. 17) are striking: the shape of the epiandrial lobes of the ninth abdominal tergum and the large, rounded, very hairy protrusion of the fused basistyles beyond the base of the aedeagus (or beyond the level of the dististyles). Not only have the epiandrial lobes a very characteristic shape in lateral aspect, but they also have rounded, incurved, spiniferous apices and an elongated dorsal concavity in each, visible from above (Fig. 18). The aedeagus is simply recurved, thick at the base but narrowing rather abruptly before mid-length. The proctiger has a slender, tapering, down-curved ventral appendage and a short, blunt dorsal one.

The male holotype of *B. patrizii* (Figs. 19-20) (Cuban Cubú, Somalia, August 1923, Patrizi; Genova) shares these characteristics. In this male, the ninth sternum and fused basistyles are carried farther backward, giving the specimen at first glance a rather different appearance from that of the type of *discors*. However, I regard this difference as one of preservation and consider the two individuals as representatives of a single species. Venation: Av absent, two Pcv. In the type of *patrizii*, the Scv in the right front wing is beyond the FRs, while in the left front wing there are two subcostal cross-veins, one before and one beyond the FRs. In the description of *discors*, Navás noted that this cross-vein was before the fork of the radial sector in the front wings (yet he illustrated it as beyond) and beyond the fork in the hind wings.

Bittacus elisabethae Navás

Bittacus elisabethae Navás 1930: 311-312, fig. 27 (wing).

Type: ♀ holotype, Elisabethville, Lubumbashi River, Belgian Congo, 4 February 1926 (1928?), M. Bequaert; Tervuren.

Range: Type locality only, vicinity of Lubumbashi (Elisabethville), southeastern Democratic Republic of the Congo.

Both Navás and Wood (1933: 523-524) compared this species with *selysi* on the basis of wing venation, noting particularly that the apical cross-vein is absent in *selysi* but present in *elisabethae*.

I have not yet been able to associate any male bittacids from the Congo region with *B. elisabethae*. The unique type specimen is generally intact; left front wing about 19.5 mm (apex of right front wing torn); pterostigma small, not conspicuously darkened; antennae black, short-haired, with apparently 22 flagellar segments; abdomen reddish brown anteriorly, darkening posteriorly, terga 6-8 brownish black; legs uniformly reddish brown, basitarsi darker brown, tarsomeres 2-5 blackish. Venation: Scv before FRs, two Pcv, cross-vein from apex of 2A to 1A bowed backward.

See also comments under *B. burgeoni*.

Bittacus fumosus Esben-Petersen

Bittacus fumosus Esben-Petersen 1913: 145, fig. 12 (wing).

Type: holotype, sex unknown (probably female; apex of abdomen missing at time of description), labelled only "Brit. O. Afr., Lindblom"; Stockholm.

Range: Kenya (unspecified type locality, also vicinity of Kitui); January. Smithers (1971) reports the species also from Tanzania, in January and February.

In a key accompanying the original description, Esben-Petersen differentiated *fumosus* from other African species on the basis of the shortness of vein 1A and absence of the apical cross-vein between Cu_2 and 1A. The de-

scription drew attention to the smoky tinge of the wings, darkest near the tip, and to darkening along certain veins and cross-veins. Esben-Petersen, in 1915, only listed the species, but in his monograph (1921: 137-138, fig. 157) he included the description and illustration of a male he regarded as belonging to *fumosus* (see below). Lestage (1917) included *fumosus* in a key and later (1929) merely listed the species. Capra (1939) compared in considerable detail the male described by Esben-Petersen with his own species, *zavattarii*.

The male that Esben-Petersen considered conspecific with the holotype of *fumosus* is in the BMNH and is labelled "Type," which of course it is not. It is also labelled "Tirva R. about 30 m. S.E. of Kitui Government Station, Ukamba Prov., Brit. E. Africa, 22-27 Jan. 1912, S. W. J. Scholefield." (Kitui is in south central Kenya, east of Nairobi, at 1°21′S, 38°01′E. There is a Tiva River southeast of Kitui, to which I suppose the label refers.) This male (Figs. 21-23), intact except for loss of the legs on the left side and two other tarsi, agrees with the holotype in wing venation, wing coloration and other comparable details. I therefore accept that it represents the same species as the holotype. As discussed under *B. alluaudi,* this specimen also closely resembles the male holotypes of *alluaudi, jeanneli* and *zavattarii* in genitalial structure, although it differs from them in the position of the Scv. The possibility of synonymy of all these species might be investigated by a detailed study of the terminalia of the Kitui male, and most appropriately by further field observations in the eastern half of Kenya.

Bittacus homburgerae Navás

Bittacus homburgeri Navás 1933b: 80-81, fig. 72 (♂ gen.).

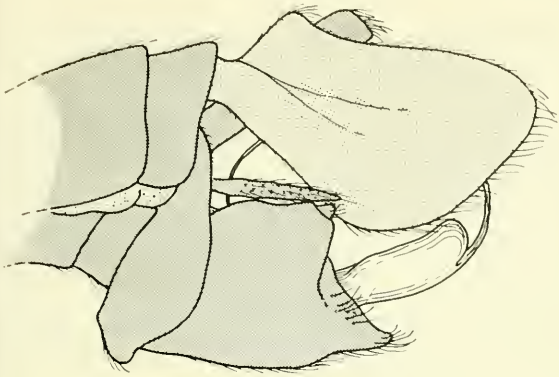
(The specific name used here is an emendation of the masculine genitive form, *homburgeri,* inadvertently used by Navás, per Recommendation 31A of the International Code of Zoological Nomenclature, 1963.)

Type: ♂ holotype, Mamou, French Guinea, June-July 1924, Mlles. Homburger and Morell; Paris.

Range: Type locality only: central Guinea. Coordinates of Mamou are 10°23′N, 12°05′W.

As far as I am aware, this species has not been mentioned in the literature on African Mecoptera since it was described.

The male holotype is in good condition except for some damage to the legs. The genital structures are not easily seen because of adhered debris, apparently grass fragments. Navás thought *homburgerae* different from other species in having blunt-tipped cerci, but I did not confirm this observation (cf. Fig. 24). The epiandrial lobes are distinctive, being elongate and bearing a broad, smooth mesal prominence and a smaller, more anterior one with a slender tuft of hairs (Fig. 25). Venation: Av present, Scv before FRs, two Pcv.



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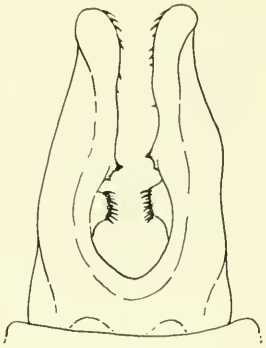

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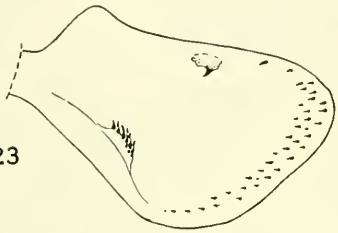

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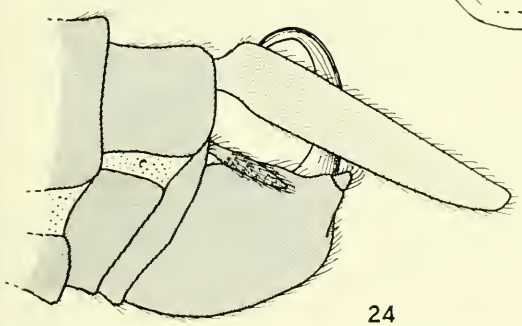

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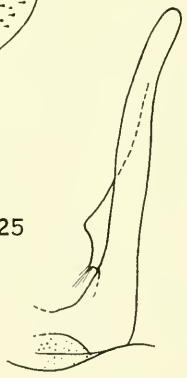

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Figs. **21-23.** *Bittacus fumosus,* male from Kitui, Kenya. **21,** terminal abdominal segments, left lateral aspect; **22,** epiandrium, dorsal aspect; **23,** right epiandrial lobe, mesal aspect. Figs. **24-25.** *Bittacus homburgerae,* male holotype. **24,** terminal abdominal segments, left lateral aspect; **25,** left epiandrial lobe, dorsal aspect. Scale line 1 mm.

If Klug (1838) had any male specimens from Senegal when he named *Bittacus testaceus*—and if he took notice of the general shape of the epiandrial lobes—this might be the form he included with specimens from South Africa in *testaceus*. There is a female in the Paris Museum from Friguiagbé, near Kindia, (French) Guinea, that I have tentatively identified as *B. homburgerae* because it is of the same general size as the holotype and has essentially the same venation and shape of wing. It was collected in 1908 by P. Prins. Friguiagbé is 9°57′N, 12°56′W, only about 40 miles southwest of Mamou.

Bittacus incertus (Navás)

Bittacus incertus (Navás) 1926b: 59, figs. 11a,b (♂ gen.), 11c (wing tip) (described as *Haplodictyus*).

This is a synonym of *Bittacus apicalis* Hagen, a North American species (see Carpenter, 1932). Navás assigned the species to *Haplodictyus,* although Banks had in 1913 synonymized that name with *Bittacus,* and Navás himself had long since relegated it to no more than a subgenus (Navás, 1914a). How Navás decided the type specimen, labelled "Wilmerding Pa.," according to him, was "apparently from Africa" is only one of many mysteries concerning his grasp of geography. Even more difficult to comprehend is his statement that *incertus* is similar to *pobeguini.* Lestage (1929), who included *incertus* in a key, also wondered about this supposed similarity.

Bittacus jeanneli Navás

See *B. alluaudi* Navás.

Bittacus kimminsi Tjeder

Bittacus kimminsi Tjeder 1956: 375-378, figs. 79 (♂ wings), 80 (♀, entire), 81-87 (♂ gen.), 88-92 (♀ gen.).

Types: ♂ holotype, ♀ allotype, Royal Natal National Park, Tugela Valley, 5250 ft., 4 April 1951, Per Brinck; Entomological Museum, University of Lund, Lund, Sweden.

Range: Natal (Royal Natal National Park; Camperdown).

This species is very similar to *B. walkeri* and was identified as *walkeri* by Esben-Petersen (1917, 1921) and Wood (1933), as explained by Tjeder (1956). Together with *walkeri* and *angulosus* it comprises a species group characterized by long, slender wings with dark veins and elongate pterostigma. Tjeder's description is detailed and his illustrations excellent, permitting easy recognition of *B. kimminsi.*

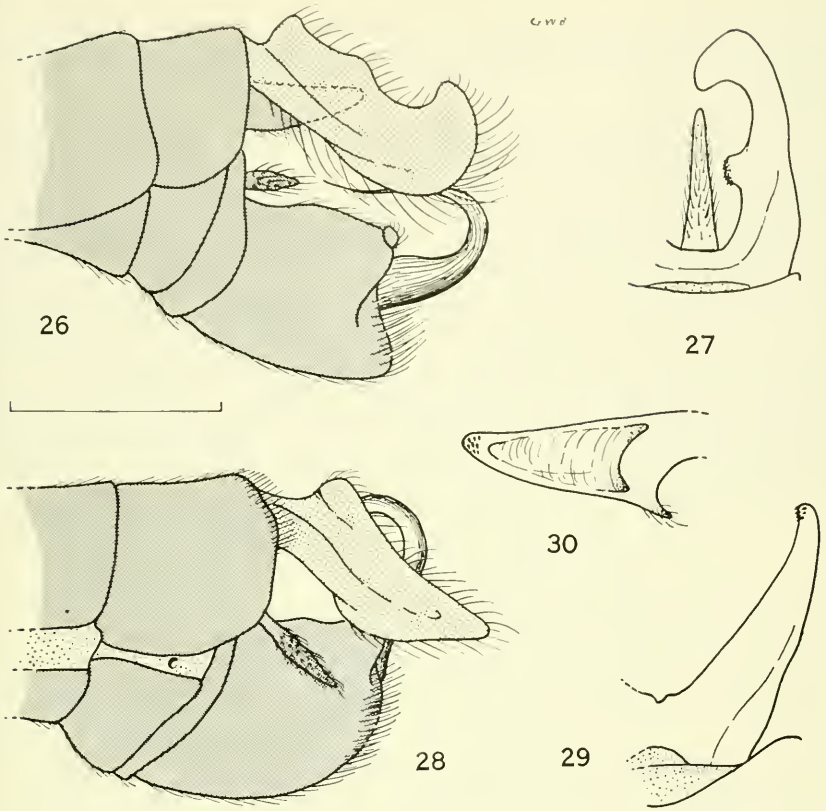
Bittacus kongoloensis Lestage

Bittacus kongoloensis Lestage 1929: 5, 11, 17 (in key); no figs.

Type: ♂ holotype, Kongolo, Belgian Congo, at light, 30 January 1911, M. Bequaert; Tervuren.

Range: Eastern Democratic Republic of the Congo (Kongolo is at 5°23′S, 27°00′E), western Tanzania; January.

In 1913, Esben-Petersen described and illustrated a male of this species under the name *Bittacus pobeguini* Navás. Lestage (1929) methodically set forth the differences between this specimen and the female holotype of *pobeguini,* then renamed the Kongolo male. The specimen described and figured by Esben-Petersen in 1921 (p. 135, figs. 152-153) as *pobeguini,* and



Figs. **26-27.** *Bittacus kongoloensis,* male holotype. **26,** terminal abdominal segments, left lateral aspect; **27,** left epiandrial lobe and part of proctiger, dorsal aspect. Figs. **28-30.** *Bittacus lachlani,* male holotype. **28,** terminal abdominal segments, left lateral aspect; **29,** left epiandrial lobe, dorsal aspect; **30,** left epiandrial lobe, mesal aspect. Scale line 1 mm.

by some subsequent authors said to be *kongoloensis,* is probably *moschinus* Navás, which he listed as a synonym of *pobeguini.*

The upturned and inwardly curved apices of the epiandrial lobes (Fig. 26) are diagnostic. Proctiger with an elongate, tapering, hairy dorsal appendage (Fig. 27). In the holotype, the cerci look short, but this is due to their being turned somewhat mesad. Neither Esben-Petersen nor Lestage commented on the pointed apex of the wings, which is even more striking than illustrated by Esben-Petersen. Venation: only one Pcv, Av absent, Scv far before FRs.

Bittacus kunenensis Wood

Bittacus kunenensis Wood 1933: 513-515, figs. 3 (wing), 4a-h (♂ gen.).

Type: ♂ holotype, Otjimbumbe, Kunene River, Southwest Africa, March 1923, South African Museum Expedition; SAM.

Range: Type locality only; Otjimbumbe does not appear in most gazetteers but is near 17°15′S, 14°30′E, on the Cunene River, northwestern Southwest Africa.

Bittacus kunenensis is still known from the holotype only. Tjeder (1956) listed the species and commented on the excellence of Wood's description and illustrations.

This is at once the most isolated and structurally one of the most unusual of the African bittacids. Each epiandrial lobe of the ninth abdominal tergum bears a small protuberance dorsally near the base, a ventral subapical prominence, and a dorsal apical one, all inwardly (mesally) curved and all armed with blackened spines. Both the dorsal and ventral appendages of the proctiger are tapering and elongate, extending beyond the epiandrial lobes. Thick at its base, the aedeagus narrows abruptly and terminates in a long, slender filament. The cerci are peculiarly constricted subapically. Venation: no Av, two Pcv, Scv before FRs.

Bittacus lachlani Navás

Bittacus lachlani Navás 1925: 78-79, fig. 8 (♂ gen.).

Type: ♂ holotype, "Afrique Orient. Angl., env. de Nairobi, Vte. de Poncins et Cte. de Lambertye, 1912"; Paris.

Range: Type locality only: vicinity of Nairobi, Kenya. See comments below.

In the original description, Navás stated that *lachlani* was similar to *selysi,* but while there are several points of similarity, there are numerous differences in venation, wing coloration, and details of male genitalia. Capra (1939) drew attention to the resemblance of his new species *boranicus* to *lachlani,* and here the similarity is close. As stated in the comments on *boranicus,* I think that species may be a synonym of *lachlani,* but it is difficult to judge the significance of observable differences when there are only two specimens involved. Lestage (1929) briefly described the venation of *lachlani.*

The epiandrial lobes (Figs. 28-30) are widely divergent and have a few black denticles on the inner surface at the apex; they are concave mesally in the distal half and have a pocket-like structure near mid-length, opening backward. There is a darkly sclerotized but not spinous point on the inner ventral margin of each lobe (similar to that described but not illustrated for *boranicus* by Capra). A prominent, rounded ridge connects the two epiandrial lobes dorsally at their base. Venation: Av present, Scv before FRs, two Pcv.

With some doubt, I have identified as *lachlani* 3 males and 3 females from Nairobi, Kenya, 20 May 1967, and 1 female from 27 mi. NW of Nairobi, 5800 feet, 10 May 1967, all collected by C. D. Michener (Snow Entomo-

logical Museum). These males have fewer blackened spines at the apices of the epiandrial lobes than in the holotype.

Bittacus leptocercus Navás

Bittacus leptocercus Navás 1934: 16, fig. 104 (♂ gen.).

Types: 1 ♂, 1 ♀ syntypes, "Ost Afrika, Tanganyika Territory, Kinanga, P. O. Mufindi, 6-VII-1932." The types were in the Zoologisches Museum, Hamburg, Germany, but were apparently destroyed during World War II.

Range: Type locality only: Kinanga, Tanzania (near Mufindi, 8°36′S, 35°17′E, about 100 km SW of Iringa); July.

Navás described this species as having large, convex basistyles bearing long curved hairs ventrally; epiandrial lobes long, slender, subcylindrical, extending beyond the basistyles; wings yellow-tinged, with pointed tips. Venation: two Pcv, Av present, Scv not mentioned. Length of fore wing, ♂, 21.5 mm, ♀, 21.8 mm. Navás' illustration of the male terminalia is not very informative but at least stirs one's curiosity about the species.

Bittacus lestagei Kimmins

See *B. schoutedeni.*

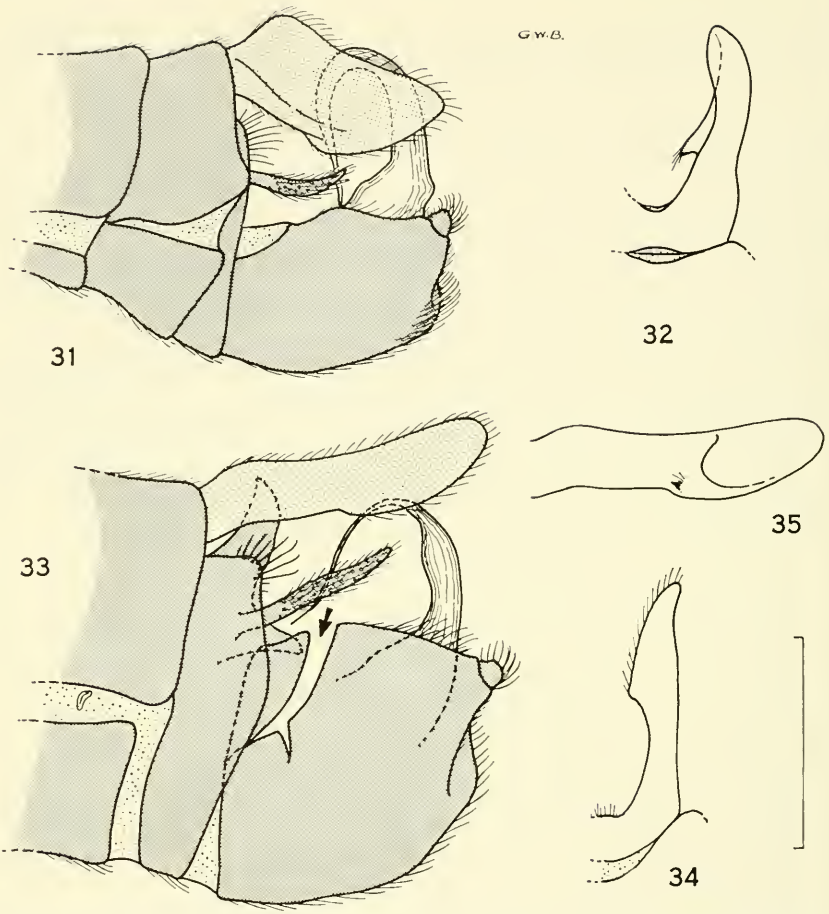
Bittacus lineatus Navás

Bittacus lineatus Navás 1914a: 48-49, fig. 24 (wing).
B. similis Kimmins 1957: 37-38, figs. 3 (wings), 4-5 (♂ gen.). New synonymy.

Type: ♀ holotype, Kijabé, British East Africa (Kenya), alt. 2100 m, sta. no. 27, 19 December 1911, Alluaud and Jeannel; Paris.

Range: Kenya: Kijabe (0°56′S, 36°34′E), Nairobi, and Ainabkoi (type locality of *similis,* 0°28′S, 35°11′E); December, June-July.

Esben-Petersen (1921) merely repeated Navás' description, and Lestage (1929) abstracted the description in a key. In 1934, Navás described and illustrated a male specimen from Nairobi, which he identified as *lineatus.* Capra (1939: 174-175) compared in careful detail the venation of this male with that of *sjostedti* and judged the former almost certainly a synonym of the latter. He supposed, however, that comparison of genitalia of this male with the male type of *sjostedti* would settle the matter. I have made this comparison and have concluded that the male from Nairobi represents a different species from *sjostedti.* Comparison of my Figures 31-32 with 45-47 will show differences in the shape of the epiandrial lobes (in both lateral and dorsal aspects) and of the base of the aedeagus. Moreover, the wings of the types of *sjostedti* are noticeably pointed at the apex, while the apex is more rounded in the Nairobi male and in the female holotype of *lineatus.* My conclusion, therefore, is that the Nairobi male called *lineatus* (Figs. 31-32)



FIGS. **31-32.** *Bittacus lineatus,* male from Nairobi, Kenya. **31,** terminal abdominal segments, left lateral aspect; **32,** left epiandrial lobe, dorsal aspect. FIGS. **33-35.** *Bittacus montanus,* male holotype. **33,** terminal abdominal segments, left lateral aspect (mounted on microscope slide, therefore rather flattened, also broken at arrow); **34,** left epiandrial lobe, dorsal aspect (from a male from Kenya); **35,** right epiandrial lobe, mesal aspect. Scale line 1 mm.

is distinct from *sjostedti* and also can be regarded as conspecific with the holotype of *lineatus.*

Bittacus similis Kimmins (1957) was described from a single male collected at Ainabko (same as Ainabkoi, I suppose), Kenya, 1 July 1948, by G. H. D. Deale; BMNH. It agrees in almost every detail with the Nairobi male of *lineatus* in lateral aspect of the male terminalia (shape of epiandrial lobe, shape of aedeagus, relative proportions, etc.) as well as in wing venation and coloration. I see differences between Kimmins' figure of the epiandrial lobes (Kimmins 1957) and my Figure 32 but think this a matter of posing

the specimens. Accordingly, I have placed *similis* Kimmins in the synonymy of *lineatus* Navás.

The difference in seasonal occurrence of the two males and the female raises some question, but similar seasonal distributions are known for other African species.

Bittacus longistigma Navás

See *B. weelei* Esben-Petersen.

Bittacus montanus Weele

Bittacus montanus Weele 1909: 21-22, fig. 4 (♂ gen., printed upside down).

Type: ♂ holotype, Kibonoto, Mt. Kilimanjaro, March (1906), Y. Sjöstedt; Stockholm.

Range: Tanzania (=Tanganyika; German East Africa), Democratic Republic of the Congo (primarily eastern half, but there is one record from "Bas Congo"), Rwanda, Uganda, Zambia (Northern Rhodesia), Rhodesia (including Mashonaland); August-December (records for every month), March-April, possibly two generations a year. Collected at elevations from 350 to 1500 meters. Kimmins (1957) records the species also from Cameroon, but I have seen no specimens from there. Esben-Petersen (1921) recorded it from Nyasaland (Malawi), but his specimen appears to me to be *schoutedeni*.

Since this is one of the earliest described African species (and the first for which we have a really useful description and illustration), there have been numerous references to it. Esben-Petersen (1913) recorded a specimen from Beni, Belgian Congo, and illustrated its venation; in 1915 he merely listed the species. Lestage (1917) discussed venational variation and the identity of several specimens (his figs. 1A-1E) and regarded *schoutedeni* as a synonym of *montanus*. His opinions were based largely on a specimen identified as *montanus* by Esben-Petersen, which he illustrated (Lestage 1917) and which Esben-Petersen apparently also illustrated (1921, fig. 144). Tjeder (1956: 364-367, figs. 52-58) redescribed the species and accurately illustrated the wings and genitalia of the holotype; he questioned whether the illustration by Esben-Petersen (1921) was of *montanus*. (I also question it and think it depicts *schoutedeni*.) Lestage (1929) synonymized the Kindu, Congo, types of *schoutedeni* with *montanus*. Accepting Lestage's (erroneous) decision on synonymy of these species, Kimmins (1957) gave the name *lestagei* to the remaining specimen of *schoutedeni*, quite accurately illustrated the typical *montanus* (his figs. 8-9), and illustrated a variant form. Navás (1924, 1930, 1936) recorded *montanus* from various localities in the Belgian Congo and Kilimanjaro vicinity. Banks (1930) also listed it from eastern Congo. Wood (1933: 517-519, fig. 7) described and illustrated the species correctly and recorded it from Rhodesia and Uganda.

Various authors have criticized Weele's illustration of the holotype although most of them had not seen it themselves. Actually, it is accurate in all important details. Other illustrations that agree with the type are those by Wood, Tjeder and Kimmins, cited above. The terminalia of the holotype have been cleared and mounted in balsam between plastic and glass. This has led to some distortion, including a break in the basistyle (Fig. 33, arrow) and the obscuring of the shape of the mesal prominence of the epiandrial lobe, except for its rather darkly sclerotized tip (Fig. 35). Whether this prominence is visible in dorsal aspect depends upon how the specimen is posed (compare my Fig. 34, Tjeder's fig. 54, Kimmins' fig. 9). Venation: Scv about half-way between ORs and FRs, two Pcv, Av present.

Bittacus moschinus Navás

Bittacus moschinus Navás 1914a: 49-50, fig. 25 (described in subgenus *Haplodictyus*).

Type: ♀ holotype, "Afrique or. allemande, Kilimandjaro, versant sudest . . . zone inferieure, Neu Moschi, 800 m, Avril 1912, st. 72," Alluaud and Jeannel; Paris.

Range: Type locality only, Mt. Kilimanjaro, northern Tanzania.

Esben-Petersen (1921: 135, figs. 152-153) described and illustrated a male that he supposed belonged to *pobeguini* and placed *moschinus* in the synonymy of *pobeguini*. This male, however, I regard as actually *moschinus* and almost surely *not* conspecific with the female holotype of *pobeguini*. Lestage (1929) also regarded *moschinus* and *pobeguini* as different species but was considering the latter in the sense Esben-Petersen had used it. Esben-Petersen (1921) further supposed that a male he had illustrated in 1913 (which later became the holotype of *B. kongoloensis*) was a "somewhat shrivelled" individual of the form illustrated in his 1921 monograph, but the two are quite distinct (cf. my Figs. 36 and 26).

In 1935, Navás described what he regarded as the male of *moschinus*. This male (Figs. 34-35), in the Paris Museum, bears the same label data as the holotype, except station 73 instead of 72, and is labelled "Typus." Navás recognized this was the same form as that illustrated by Esben-Petersen in 1921 (as *pobeguini*). He remarked that the shape of the genital appendages would permit instant separation of *moschinus* from the true *pobeguini,* which is rather curious since *pobeguini* was then and still is known from the female holotype only.

Since the male described by Navás is from very near the type locality and since it does agree with the type in most comparable details, I accept it as representing the species *moschinus*. It has only one leg and one antenna left, but wings and body are generally intact. It is noticeably larger than the holotype female (front wing 22 mm, only 17 mm in the type), has the Scv somewhat before the FRs, and has no Av. Navás illustrated the left front

wing of the holotype, which has the Av present, but noted it was absent on the right side. Both specimens have the acute wing tip and single Pcv. The epiandrial lobes appear rather simple in lateral aspect (Fig. 36), slightly upturned beyond mid-length, with rounded apex. In dorsal aspect (Fig. 37) they are more complex, with a subapical, inwardly-directed spiniferous projection, a more blunt, spiniferous tubercle nearer the base, and a broadly rounded portion of the ventral margin bearing a tuft of hairs. The aedeagus is thick and swollen at the base, narrows rapidly, and appears to be broken off a little beyond mid-length.

Bittacus natalensis Wood

Bittacus natalensis Wood 1933: 510-512, figs. 1 (wings), 2 (♂ gen.).

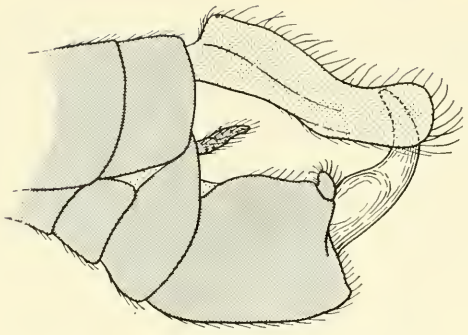
Types: ♂ holotype, ♀ allotype, both from Bulwer, Natal, 1914, W. Haygarth; SAM.

Range: Natal (Bulwer, 29°48′S, 29°46′E), Rhodesia (Southern Rhodesia), Transvaal; January-March.

Capra (1939) briefly compared his new species *zavattarii* with *natalensis,* noting that these forms, together with *alluaudi, jeanneli* and *fumosus,* comprised a group sharing many similar characters. Tjeder (1956: 369-371, figs. 63-70) illustrated details of a male and a female from Transvaal that he supposed were the same as Wood's types from Natal, although he recognized that there were some differences, particularly in the proctiger of the male. In 1961, Smithers recorded several specimens of *natalensis* from the lower Lundi River, Southern Rhodesia.

Venation: Av absent, one or two Scv before or one before and one beyond FRs, two Pcv.

The differences between the descriptions and illustrations provided by Wood and Tjeder are easy to see but not so readily interpreted. My evaluation of them is hampered by the fact that I have not seen the specimens involved. The presence in southern Africa of yet another very similar yet different form (*zambezinus* Navás) complicates the evaluation. That is, clearly there are in southern Africa representatives of a species group characterized by such structures as large penunci at the base of the long, coiled, filamentous aedeagus, an enlarged, thickened proctiger with long, slender ventral appendage, and broad epiandrial lobes with two spinose projections on the inner surface. But does this group comprise two or three species? Wood showed an elongate dorsal appendage on the proctiger of *natalensis,* which he described as a "stout, cylindrical, membranous filament, spoon-shaped apically." Tjeder's specimen has this appendage considerably more enlarged at the tip and bilobed, and with a rounded, hairy accessory projection beneath its base. The membranous nature of the main body of the proctiger makes difficult the evaluation of obvious differences in the shape of



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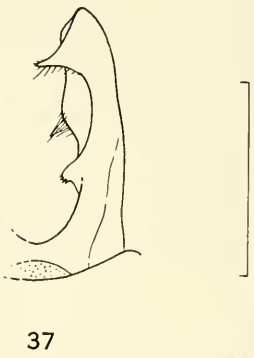

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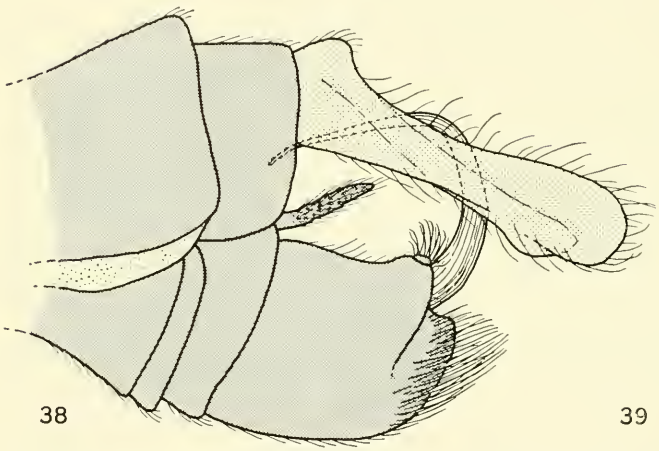

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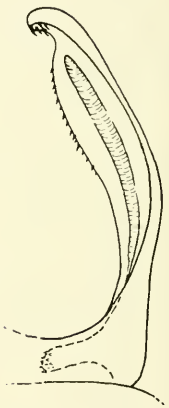

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FIGS. **36-37.** *Bittacus moschinus,* topotypic male. **36,** terminal abdominal segments, left lateral aspect; **37,** left epiandrial lobe, dorsal aspect. FIGS. **38-39.** *Bittacus nebulosus,* male from "Caffraria." **38,** terminal abdominal segments, left lateral aspect; **39,** left epiandrial lobe, dorsal aspect. Scale line 1 mm.

this structure in the two males in question. In summary, this is a problem that can be investigated by a study of additional specimens from the region involved and determination of the extent of variation that can be accepted as intraspecific. This species needs also to be compared in detail with *zambezinus.*

Bittacus nebulosus Klug

Bittacus nebulosus Klug 1838: 99-100; no figs.

Type: 1 specimen, sex unknown, "vom Kap," (no date). The type lacked the apex of the abdomen at the time of description; Berlin. In 1964 I found the type, in the Berlin Museum, completely destroyed by dermestids.

However, since the identity of the species has not been and is not in doubt, I think it unnecessary to designate a neotype. Tjeder (1956: 352) restricted the type locality to Eshowe, Zululand (northeastern Natal, 28°54′S, 31°28′E).

Range: Natal, Transkei (Caffraria), eastern Cape Province, Transvaal, and Mozambique; November-January. Tjeder (1956) lists numerous specific localities and dates. I have recently seen specimens from Mariepskop, Transvaal (west of Kruger National Park, 24°25′S, 30°51′E), and 5 miles NW of Pietermaritzburg, Natal, all taken in December.

In the first 70 years after its description, *nebulosus* was only briefly mentioned by Walker (1853), and the first additional information about it was the report of its occurrence at Guengère and Valley of Pungoné, Mozambique (Navás 1909). Both Banks (1913) and Lestage (1917) included it in keys; so did Esben-Petersen (1913), who also illustrated the wing and recorded *nebulosus* from Caffraria. In 1915, Esben-Petersen only listed the species, but in his 1921 monograph he illustrated both the venation and male genitalia. Lestage (1929) compared *nebulosus* with *peringueyi* and questioned the validity of *Haplodictyus* on the basis of specimens of *nebulosus*. Wood (1933) redescribed the species, pointing out some errors in earlier descriptions, added Natal to known localities, and illustrated the male genitalia. The female was first illustrated by Tjeder (1956), who also summarized the known range.

Wood's illustration of the male terminal abdominal segments (1933: 520, fig. 8) was drawn in lateral aspect from a KOH-cleared specimen. He drew attention to the elongate process on the inner surface of each epiandrial lobe, which is normally concealed by the basal part of the ninth tergum (cf. my Fig. 39, where this is indicated by a broken line). But he, as well as earlier authors, omitted mention of the peculiar long, thick fold that crosses the mesal surface of the epiandrial lobe diagonally and is joined to the lobe proper by a thin cuticular connection, producing an elongate trough (Fig. 39). The specimen illustrated here (Fig. 38) from Caffraria, had no blackened denticles above this thickened fold, except at the incurved apex, while Wood showed these denticles rather diffusely distributed on the apical half of the lobe. A somewhat similar form of epiandrial lobe, that is, with such a trough visible in dorsal aspect, is seen also in *B. weelei* and *B. stanleyi*.

This large South African *Bittacus* may be recognized by the strongly yellowish brown tinged wings with grayish brown clouding along many cross-veins and near the stigma. The central African *B. stanleyi*, however, has strikingly similar wings. Venation: Av absent, Scv beyond FRs, two Pcv.

Bittacus negus Navás

See *B. weelei* Esben-Petersen.

Bittacus oreinus Navás

Bittacus oreinus Navás 1914b: 89-90, fig. 6 (wing).

Type: ♀ holotype, "Aethiopia merid. Mons. Zyqual, Maurice de Rothschild, 1905"; Paris.

Range: Type locality only: southern Ethiopia, Mount Zyqual (the volcano, Mt. Ziḱ-Wala, or Zukwala, 8°32′N, 38°49′E, about 58 km SSE of Addis Ababa).

When he described *oreinus*, Navás judged it similar to *montanus* Weele, and subsequent authors have been unable to deal with the species any more effectively. Esben-Petersen (1921) merely repeated the description. Lestage (1929) redescribed the type, illustrated one of its hind wings (indicated as a front wing), analyzed the venation in detail, but was unable to conclude that *oreinus* was a synonym of *montanus*. Capra (1939) pointed out similarities between *oreinus* and his new species, *boranicus* and *berlandi*.

This is another instance of the need for further specimens from the type locality. It seems unlikely that very many species of *Bittacus* exist on Mt. Zukwala; therefore, capture of similar males would do much to clarify the status of the unique type. Venation: two Pcv, Scv about mid-way between ORs and FRs, Av present.

Bittacus patrizii Navás

See *B. discors* Navás.

Bittacus peringueyi Esben-Petersen

Bittacus peringueyi Esben-Petersen 1913: 144, fig. 11 (♂ gen.).

Type: ♂ holotype, King William's Town, eastern Cape Province, South Africa, April 1894, Lightfoot; SAM.

Range: Eastern Cape Province, Natal and Transvaal. Tjeder (1956: 368) listed numerous localities; February-April, and one record for June.

The original description of *peringueyi* differentiated the species from others then known from Africa, by means of a key. In 1915, Esben-Petersen only listed the species, but in 1921 he redescribed it and illustrated both the wings and male genitalia. Lestage (1917) included it in a key; later (1929) he contrasted it with *nebulosus* and correctly pointed out Navás' misidentification of *peringueyi* as *Haplodictyus testaceus*. An accurate, detailed illustration of the male terminal segments accompanied Wood's (1933) treatment of the species. Tjeder (1956) illustrated the wings and details of the female reproductive structures.

B. peringueyi is easily identified among South African species by the venation (only one Pcv, Av present, Scv only a little beyond ORs) and conspicuous, subtriangular stigma. The male is characterized by elongate, taper-

ing epiandrial lobes bearing a few blackened denticles on the inner surface near the tip and a thick, rounded mesal projection near the base.

Bittacus peterseni Kimmins

Bittacus peterseni Kimmins 1938: 293-294, figs. A (wings), B-D (♂ gen.).

Type: ♂ holotype, Chuda River, East London, Cape Colony, 4 November 1923, H. K. Monro; BMNH.

Range: Type locality only, eastern Cape Province, Republic of South Africa; November.

Kimmins characterized this species as generally "similar to *B. selysi*, but larger, and with narrower wings." The pointed mesal projection at the lower edge of each epiandrial lobe is broader at the base than in *selysi* and is directed inward so as to be visible in dorsal aspect, while in *selysi* it is concealed. The cerci in the holotype are somewhat dilated apically. Kimmins (1938) provided illustrations of the wings and details of male genitalia of *selysi* as well as of *peterseni*, for purposes of comparison. Venation: Av absent, Scv a little beyond ORs, two Pcv. Clouding along cross-veins r-m, 1st m, and m-cu, near ORs, at FRs, and at origin of M.

Tjeder (1956) listed the species but had not seen the unique type.

Bittacus pinguipalpi Wood

Bittacus pinguipalpi Wood 1933: 515-517, figs. 5 (wings), 6a-c (♂ gen., maxillary palp).

Type: ♂ holotype, Narebis, South-west Protectorate, February 1921, K. H. Barnard; SAM.

Range: Type locality only, in Southwest Africa (approximately 20°12′S, 16°45′E); February.

Wood described and illustrated the unique holotype in excellent detail. Tjeder (1956) listed the species but had not seen it.

Like the only other *Bittacus* from Southwest Africa, *kunenensis*, this species is structurally set quite apart from African bittacids generally. The maxillary palps have a very small, tapering apical segment and are densely pubescent. The epiandrial lobes, only about half as long as the fused basistyles, are somewhat trapezoidal, each with a blunt, hair-tipped projection near the middle of the concave mesal surface and a few short blackened spines on the inner surface near the apex. Venation: Av absent, two Pcv, Scv just before FRs in front wing, half-way between origin and FRs in hind wing.

Bittacus pobeguini (Navás)

Bittacus pobeguini (Navás) 1908: 414 (p. 16 in reprint), fig. 16 (wing) (described as *Haplodictyus*).

Type: ♀ holotype, "Baoulé, en la costa de Marfil," 1897, H. Pobeguin; Paris.

Range: Type locality only: this seems to be Baoulé So, a town at 6°35′N, 5°53′W, in the south-central "costa de Marfil" region of the Ivory Coast.

Navás (1909) merely listed the species. In 1913, Esben-Petersen illustrated (gen., wing) and described a male from Kongolo, Belgian Congo, which he identified as *pobeguini*. This specimen was later made the holotype of *kongoloensis* by Lestage (1929), who compared it in detail with the female type of *pobeguini*. Esben-Petersen (1915) only listed *pobeguini*, and Lestage (1917) included it in a key. In his monograph (1921), Esben-Petersen illustrated another male that he supposed was *pobeguini*, and synonymized *moschinus* with *pobeguini*. Lestage (1929) rejected this synonymy; I agree with him and think the male shown by Esben-Petersen (1921) is the true *moschinus* (which see). Thus, although two different males have been described as *pobeguini*, neither is, and the species remains known only from the holotype female.

Bittacus pobeguini has the subtriangular stigma, single Pcv, and lacks the Av, as in *B. chevalieri*, also from West Africa. This brings up the matter of how to differentiate these two species. A comparison of the holotypes shows that *pobeguini* is slightly the smaller (front wing 16.5 mm), has somewhat more acutely tipped wings, and has less darkly colored wings. Color differences described by Navás are probably not diagnostic.

Bittacus rhombicus Kimmins

See *B. berlandi* Capra.

Bittacus schoutedeni Esben-Petersen

Bittacus schoutedeni Esben-Petersen 1913: 143-144, figs. 9 (♂ gen.), 10 (wing).
B. lestagei Kimmins 1957: 40 (new name for *schoutedeni*, in part). New synonymy.

Types: 1 ♂, 1 ♀ syntypes, ". . . Congo Belge, Kilom. 345 du Kindu, Dr. Russo, la nuit"; Tervuren. The male is hereby designated lectotype. There was originally also a teneral male from Mufungwa, Congo, 20 November 1911, Dr. Bequaert, that can be considered a syntype. In 1921, Esben-Petersen stated that the Kindu specimens were the types of *schoutedeni*, and he listed the teneral male as merely another specimen of this species. The excluded Mufungwa male was later made holotype of *B. lestagei* by Kimmins; its present whereabouts is unknown.

Range: Democratic Republic of the Congo. The locality datum for the types is not very informative, for we are not advised 345 kilometers in what direction from Kindu. One may suppose that prior to 1913 it must have been either 345 km down the Lualaba River by boat (which would be near Stanleyville) or up the river by railroad to the vicinity of Kabalo. But it is not important, for *schoutedeni* has been recorded from such widespread parts of the country as Sandoa (on the Lulua River in western Katanga),

Vieux Kasongo (in southwestern Kivu, 4°30′S, 26°35′E), Beni (Ruwenzori region, 0°20′N, 29°40′E), and Lubumbashi (11°45′S, 27°40′E). I have recently seen male specimens from Lubumbashi (at light, 8 December) and Kasenga (31 December); December, April. The Mufungwa locality, also called Sampwe, is at 9°30′S, 27°25′E.

In 1915, Esben-Petersen listed the species. Lestage (1917) regarded *schoutedeni* as a synonym of *montanus* Weele, calling attention to differences in venation between the male and female (Kindu) types and concluding that the epiandrial lobes in the male had dried in a bent or twisted position that made them seem different from those of *montanus*. He accurately illustrated the left epiandrial lobe of the male type in dorsal aspect. Esben-Petersen (1921) redescribed and again illustrated *schoutedeni*. In 1929, Lestage once more compared *montanus* and *schoutedeni*, discussing specimens from various localities in his characteristically lively and entertaining style. He again concluded that the Kindu specimens were in fact *montanus* but that the Mufungwa male (see Types, above) was the true *schoutedeni*. And he revealed the ways in which it differed from the Kindu male.

Kimmins (1957) accepted this synonymy and pointed out that if the Kindu specimens were the types, as stated by Esben-Petersen, the Mufungwa ("Mafunga") male required a new name, which he supplied (*Bittacus lestagei* Kimmins). The Mufungwa male was borrowed from Esben-Petersen by Lestage, but I have not been able to locate it, either in the Esben-Petersen collection in Copenhagen or in the collections in Brussels or Tervuren. It seems to me virtually impossible that the Kindu male type (lectotype) of *schoutedeni* E.-P. and the Kilimanjaro male holotype of *montanus* Weele could represent the same species (compare Figs. 40 and 33). Under the circumstances, I think *lestagei* Kimmins should be relegated to synonymy of *schoutedeni*.

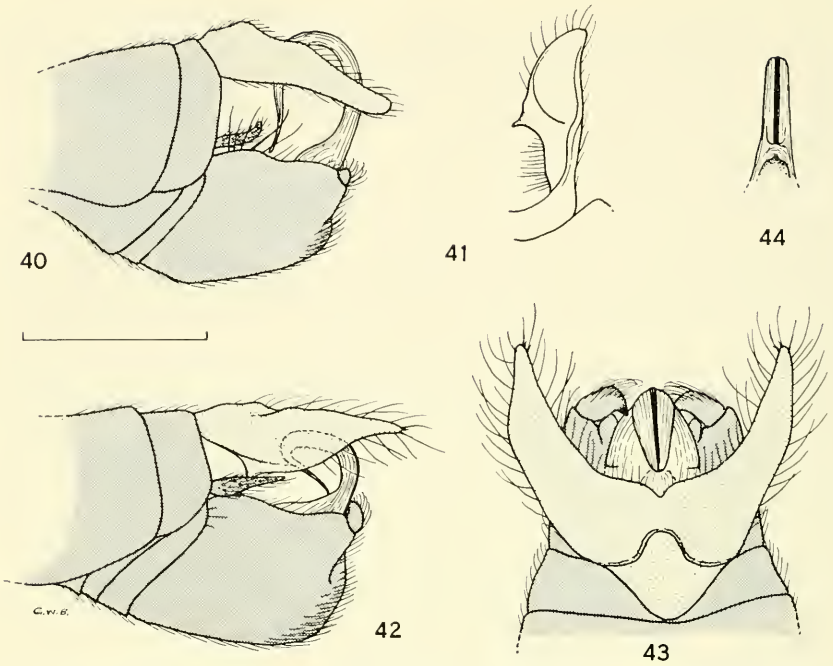
The lectotype of *schoutedeni* (Figs. 40-41) is more slender than males of *montanus*, has much smaller basistyles, and has an evenly tapering aedeagus. The epiandrial lobes are indeed somewhat twisted, as observed by Lestage, but bear at the ventral margin a relatively large, not densely sclerotized point (Fig. 41) rather than the smaller, blackened one seen in *montanus*. In Figure 40, the left cercus appears shorter than it actually is because its tip is curved mesad. Venation: Av present, Scv about half-way between ORs and FRs, two Pcv.

Bittacus selysi Esben-Petersen

Bittacus selysi Esben-Petersen 1917: 187-188, figs. 1 (wings), 2 (♂ gen.).

Types: ♂ holotype, Port Natal (=Durban) (no other data); Brussels. One ♂ paratype, Durban, Natal, July 1913, W. Haygarth; SAM.

Range: Coastal Natal at Durban, Zululand; July, December. To this, I



FIGS. 40-41. *Bittacus schoutedeni,* male lectotype. **40,** terminal abdominal segments, left lateral aspect; **41,** left epiandrial lobe, dorsal aspect (somewhat rotated). FIGS. 42-44. *Bittacus selysi,* male holotype. **42,** terminal abdominal segments, left lateral aspect; **43,** same, dorsal aspect; **44,** basal portion of aedeagus, posterior or caudal aspect. Scale line 1 mm.

can add 3 ♂, 2 ♀ from 5 miles northwest of Pietermaritzburg, Natal, 19 December 1966, C. D. Michener (Snow Entomological Museum, University of Kansas).

In his monograph (1921), Esben-Petersen summarized the original description, again illustrated the male terminalia as well as the whole insect (less left wings and legs; his plate 2, fig. 21), and compared *selysi* to *montanus*. Lestage (1929) did not know the species and only listed it. Navás (1930), in describing *B. elisabethae,* regarded it as similar to *selysi* in wing shape. Wood (1933) recorded 1 ♂, 2 ♀ of *selysi* from M'fongosi, Zululand, December 1916. He described and illustrated the male genitalia in detail, and seemed to accept the synonymy of *elisabethae* with *selysi* although he did not state it. In describing *B. peterseni,* Kimmins (1938) contrasted it with the similar *selysi* in a useful series of drawings of both species. Tjeder (1956) summarized collection data but had not seen specimens of *selysi.*

The epiandrial lobes are widely divergent (Fig. 43) and wide enough near mid-length to conceal, in dorsal aspect, the prominent ventro-mesally directed point seen in lateral view (Fig. 42). Although Wood (1933) de-

scribed the aedeagus as "uniformly wide for three-quarters of its length, then tapering to a sharp point," I found it (at least in the holotype) very broad at its base (between the basistyles, Fig. 43), then tapering evenly (Figs. 43-44) through mid-length, and abruptly narrower in the apical one-third. Venation: Av absent, Scv about half-way between ORs and FRs, two Pcv.

Bittacus similis Kimmins

See *B. lineatus* Navás.

Bittacus sjostedti Weele

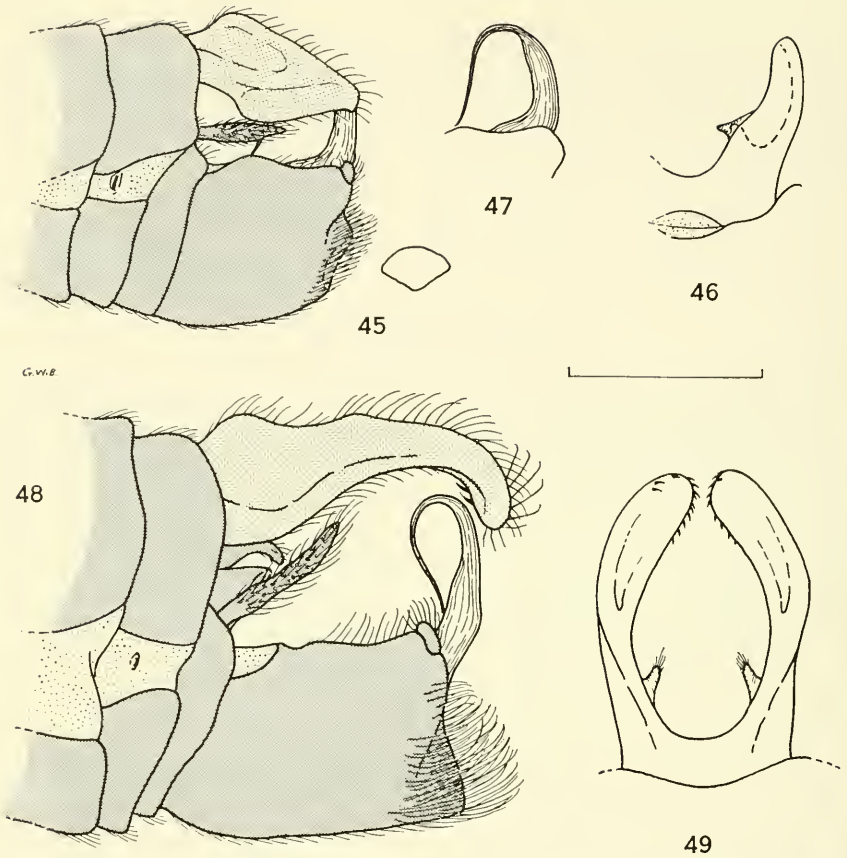
Bittacus sjostedti Weele 1909: 22, fig. 5 (♂ gen., printed upside down).

Types: 1♂, 3♀ syntypes, Kilimanjaro, German East Africa (Tanganyika), 1905-1906, Yngve Sjöstedt, Swedish Zoological Expedition. Weele gave the date 18 September for the male, and for the females the further data: Kibonoto, 1000-1300 m, 27 April; 1300-1900 m, 29 April; rain forest, 2000 m, 5 January. The male and one female are in the Riksmuseet, Stockholm. The male is hereby designated lectotype. It is labelled "Kilimandjaro, Sjöstedt, 1905-6" and "*Bittacus sjöstedti*, Type, Weele" and bears the number 186 on a pink tag (a collection-date code, I assume). The lectotype is intact except for lacking both front legs, right middle leg, and both antennal flagella.

Range: Northern Tanzania, Kenya; January, April, September.

Esben-Petersen (1913) included *sjostedti* in a key and in 1915 merely listed it. Navás (1914a) recorded additional specimens from Neu-Moschi, German East Africa (Kilimanjaro) in April, and from Nairobi, Kenya. In 1921, Esben-Petersen repeated the original description and commented on the venation. Lestage (1917) included *sjostedti* in a key; in 1929 he chided Navás for not commenting more on details of venation and genital structure, though he himself had nothing to contribute. By far the best description of *sjostedti* is that by Capra (1939), who discussed and illustrated the wings and terminalia of the male type ("olotipo") and wings of the female ("paratipo") in the Stockholm Museum. He correctly grouped *sjostedti* with *selysi, peterseni, lachlani* and his own new species, *berlandi* and *boranicus*. In his discussion of *B. lineatus*, Capra expressed a strong suspicion that it is a synonym of *sjostedti*.

Figures 45-47 show details of the terminal abdominal segments of the male lectotype. At the end of the fused basistyles there is a peculiar, shallow excavation, indicated by a broken line in Figure 45 (its shape in posterior aspect shown as inset). Each epiandrial lobe is concave mesally from apex to near mid-length, where a flange or ridge extends dorsad from a smooth, pointed projection near the ventral margin (Fig. 46). The aedeagus, stout at base, becomes abruptly slender near mid-length (Fig. 47). The apex of the



FIGS. **45-47.** *Bittacus sjostedti,* male lectotype. **45,** terminal abdominal segments, left lateral aspect (inset—caudal aspect of depression in fused basistyles); **46,** left epiandrial lobe, dorsal aspect; **47,** aedeagus, left lateral aspect. FIGS. **48-49.** *Bittacus stanleyi,* male holotype. **48,** terminal abdominal segments, left lateral aspect; **49,** epiandrium, dorsal aspect. Scale line 1 mm.

wing is evenly rounded to the end of R_5, then more nearly straight, producing a somewhat pointed tip. Venation: Av present (two in right hind wing of lectotype), Scv before FRs, two Pcv. There is dark clouding along most cross-veins, at origins of M and Rs, first fork of M, etc., and the wing apex is infuscated.

Bittacus sobrinus Tjeder

Bittacus sobrinus Tjeder 1956: 381-382, figs. 99 (wings), 100-106 (♂ gen.).

Type: ♂ holotype, Underberg, Natal, 24 November 1941, L. Bevis; Durban.

Range: Type locality only: southwestern Natal, Republic of South Africa (Underberg is at 29°47′S, 29°30′E); November.

This species has not been recorded in the literature since it was described.

Generally similar to males of *selysi* and *peterseni*, that of *Bittacus sobrinus* may be distinguished most readily by the shape of the epiandrial lobes. These are turned upward and slightly inward in the apical half, somewhat as in *woodi*, but are toothed at the extreme tip. On the lower margin near mid-length is a mesally directed conical projection bearing a few hairs, and from this a prominent flange extends upward across the inner face of the lobe. Tjeder (1956) illustrated these and other details and described color differences, summarized in a key (p. 382), to differentiate *sobrinus*, *selysi* and *peterseni*. Venation: Av absent, Scv in front wing about mid-way between ORs and FRs, two Pcv.

Bittacus solitarius Tjeder

Bittacus solitarius Tjeder 1956: 363-364, figs. 47-51 (♀ gen.).

Type: ♀ holotype, Caffraria, J. Wahlberg (no other data); Stockholm.

Range: Eastern Cape Province of Republic of South Africa, Rhodesia; December.

The holotype of *solitarius* had been identified by Esben-Petersen (1921) as *testaceus*. Tjeder's fine illustrations show in detail the structural differences between this specimen and females of *testaceus* (as *brincki*) and *armatus*, the latter having the greater similarity to *solitarius*. Smithers (1960) identified as *solitarius* two males (and four females) from Inyanga (18°13′S, 32°46′E) and Umtali (19°00′S, 32°40′E), Southern Rhodesia. These closely resemble *armatus*, differing primarily in the shape of the mesal projections near the bases of the epiandrial lobes. Venation: Av present, Scv just before FRs, two Pcv.

The holotype is badly damaged, lacking both antennae and five of its legs; wings present but very dirty; abdomen broken off, but parts of it attached to pin below specimen.

Bittacus stanleyi Byers

Bittacus stanleyi Byers 1968: 34-36, figs. 1 (wings), 2-3 (♂ gen.).

Types: ♂ holotype, upper Nyakagera River, Kabare region, eastern Kivu province, Congo (about 42 km WNW of Kabare, 2°25′S, 28°27′E), elev. 1600 m, November 1955, G. Marlier; Tervuren. Paratypes: 2 ♂.

Range: Democratic Republic of the Congo (type locality in Kivu; Kashusha, western Kivu; Eala, western Equateur province, 0°04′N, 18°17′E); November.

This species appears to combine the large size and strongly tinged and clouded wings of *B. nebulosus* with genitalial characters much like those of *B. weelei*. The epiandrial lobes are narrowed and curved downward (Fig. 48) and have a glabrous longitudinal mesal ridge or flange separated from

the lateral part of the lobe by a shallow trough (Fig. 49), somewhat as in *nebulosus* but more as in *weelei*. Venation: Av present, Scv near end of Sc, well beyond FRs, two Pcv.

Bittacus testaceus Klug

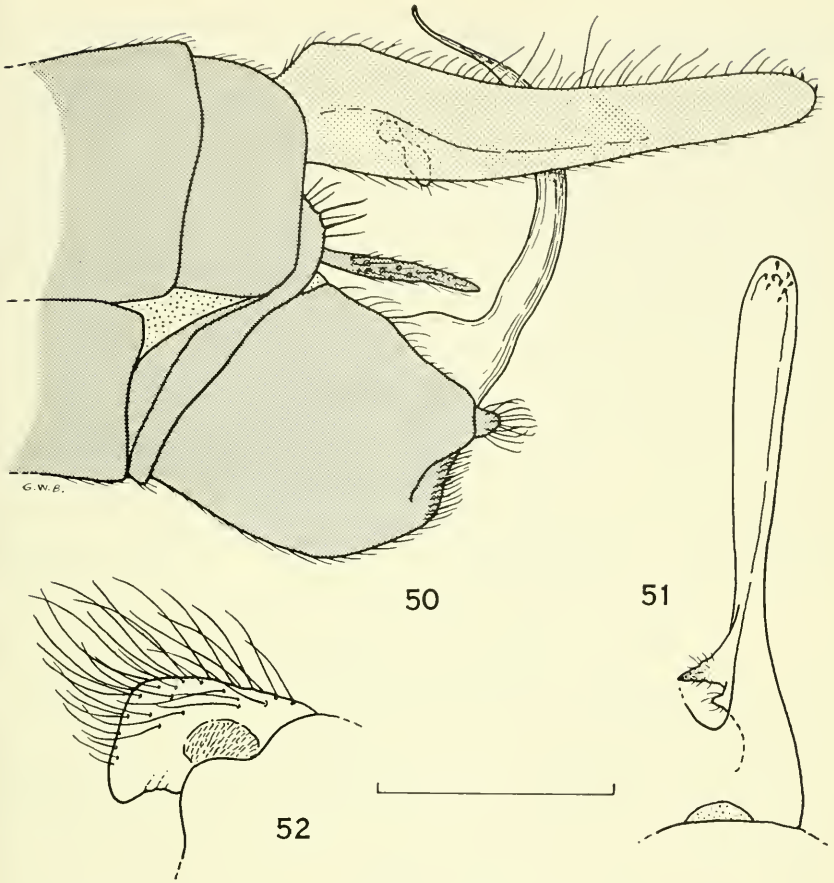
Bittacus testaceus Klug 1838: 98 (no fig.).
B. brincki Tjeder 1956: 355-360, figs. 16-17 (wings, ♂, ♀), 18-21 (venational variation), 22-28 (♂ gen.), 29-33 (♀ gen.). New synonymy.

Types: 1 ♂, 1 ♀, 1 broken syntypes, "Cap der guten Hoffnung, Krebs"; Berlin. The male is hereby designated lectotype. In addition to the locality-collector label, the lectotype is labelled "*Bittacus testaceus* Klug" and "Type" (on a red tag); there is also a small label bearing the number 216, and to all these I have added a lectotype label. The front and middle legs of this specimen are damaged or missing; hind legs, antennae and wings are intact. The abdomen was dried in a distorted position, but I have cut off the terminal segments, softened them in boiling water, and restored them to more or less their original form. Klug mentioned specimens "vom Kap und eben so vom Senegal," but I have not been able to locate any syntype(s) from Senegal.

Range: Transvaal, Natal, possibly also Mozambique and Rhodesia; December-January. Since this was one of the first species described from Africa, many early specimens from various parts of the continent were referred to *testaceus*. In fact, as shown by Tjeder (1956), even several of the more recent records of *testaceus* actually pertain to other species.

Walker (1853) was the only author to mention *testaceus* for 70 years after it was described, and he only listed it. Weele (1909) recorded it with doubt from Kilimanjaro, and his specimens were subsequently made types of *weelei*. Navás (1909) reported *testaceus* from Abyssinia (surely in error) and Mozambique (possibly correctly). Enderlein (1910) listed the species from Transvaal. In 1913, Esben-Petersen included it in a key and mentioned specimens from Caffraria and Transvaal; his figure of the male genitalia—the first published—agrees with the lectotype designated above, and his description of *weelei* in the same paper stated that he had seen the types of *testaceus* in Berlin. Banks (1913) discussed the venation and included *testaceus* in a key. Also in 1913, Navás identified as "*Haplodictyus testaceus*" a specimen later correctly identified as *B. peringueyi*. Esben-Petersen (1915) listed *testaceus* and later (1921) redescribed it and illustrated the wings and male terminalia; some of his listed localities pertain to *armatus* Tjeder.

In 1917, Lestage only mentioned *testaceus* in a key, but in 1929 he dealt at some length with the confusion of this with other species. Reviewing the problem of supposed widespread occurrence of *testaceus*, he mentioned a specimen of it from Senegal in the Berlin Museum and later said (my translation), "If therefore one sets aside the specimens from Senegal (Klug's



Figs. **50-52.** *Bittacus testaceus,* male lectotype. **50,** terminal abdominal segments, left lateral aspect; **51,** left epiandrial lobe, dorsal aspect (slightly rotated); **52,** right dististyle, posteroventral aspect. Scale line 1 mm, applies to Figs. **50-51** only.

types) and those from South Africa studied and reviewed by Banks, Esben-Petersen, and Enderlein, the following material remains to be looked at again:" (and there followed a list of specimens from Abyssinia and Mozambique). Tjeder (1956: 356) interpreted Lestage's parenthetical reference to Klug's Senegal specimen(s) as the designation of a lectotype and restriction of the type locality. Accordingly, he renamed the South African form *brincki.* However, I cannot agree with Tjeder that this was Lestage's intent at all, nor do I consider that Lestage technically designated a lectotype. There is, in fact, no real evidence that Klug's specimen(s) from Senegal actually still existed in 1929. Tjeder (1956) was also troubled by Klug's (1838) statement that *B. testaceus* and *nebulosus* were about the same size, for the latter

is a large species with fore wing length 26-28 mm. But the male syntype that I have designated lectotype of *testaceus* has a wing length of 26 mm.

Wood (1933) recorded *testaceus* from Natal and Southern Rhodesia and illustrated the terminal abdominal segments of a male from Transvaal. (The Rhodesian specimen may be *armatus*.) Tjeder (1956) regarded this male as not *testaceus* (i.e., *brincki*) because the epiandrial lobe was too short, its basal tooth too long. Upon comparing ratios of measurements, I regard these differences as minor, in view of the many important points of agreement in the males illustrated by Tjeder and Wood. Smithers (1959) questioned the occurrence of *testaceus* in Southern Rhodesia.

The designated lectotype (Figs. 50-52) is in agreement, I think, with the concept of *testaceus* held by Ebsen-Petersen, Lestage and Wood. In this specimen, the eighth abdominal sternum (Fig. 50) remains badly distorted and the basistyles, as shown, somewhat less so. The epiandrial lobe (Fig. 51) has been rotated slightly from dorsal aspect to reveal the mesal projections; the number of apical spines varies from one individual to another and between lobes in one male (8, 9 in lectotype). Venation: Av present, two Pcv, Scv before FRs.

Bittacus tjederi Londt

Bittacus tjederi Londt 1970: 53-55, figs. 1-10 (wings, head and thorax, ♂ gen., ♀ gen.).

Types: ♂ holotype, ♀ allotype, 20 ♂, 15 ♀ paratypes, Goedehoop (a farm), Heidelberg District, Cape Province, South Africa, October 1951, C. P. Museum Expedition; SAM.

Range: Known only from the type locality in Cape Province, Republic of South Africa (Heidelberg is at 34°05′S, 20°57′E, about 145 miles east of Cape Town); October.

When he described *tjederi,* Londt compared it with *B. capensis* in numerous details. He carefully illustrated diagnostic features of males and females of both species as well as several venational variations. The two species are evidently closely related yet distinct. They have in common, besides general size and color, some rather striking shining black markings on the dorsum of the head and thorax. *B. tjederi* differs from *capensis* in details of the shape of the aedeagus (Londt illustrated but did not describe projections of the straight basal portion of the aedeagus at each side of the slender apical portion), epiandrial lobes (sharp tips abruptly hooked inward) and proctiger (smaller and more simple than in *capensis*). Venation: Av present, Scv between ORs and FRs, two Pcv.

Bittacus vumbanus Smithers

Bittacus vumbanus Smithers 1960: 46-49, figs. 1 (wing), 2, 4 (♀ gen.), 3, 7 (♂ gen.).

Types: ♂ holotype, ♀ allotype, 7 ♂, 8 ♀ paratypes, all from Vumba Mountains, near Umtali, Southern Rhodesia, 21 December 1958, A. S. and

C. N. Smithers; holotype, allotype, 1 ♂, 2 ♀ paratypes in Smithers collection (Sydney, Australia, as of 1971); other paratypes in BMNH, Tervuren, National Museum in Bulawayo, and elsewhere, as listed by Smithers.

Range: Type locality only: Rhodesia, just southeast of Umtali, about 19°07′S, 32°46′E; December.

Bittacus vumbanus resembles *nebulosus* in wing color but is a much smaller species differing greatly in genitalial structure. The epiandrial lobes are approximately parallel-sided but rounded at apex, extending backward to the level of the dististyles, each having a little beyond mid-length a low, broadly conical mesal projection with densely sclerotized tip, and at the anterior base of this a smaller tubercle bearing several hairs. Venation: Av present, Scv between ORs and FRs, two Pcv.

Bittacus walkeri Esben-Petersen

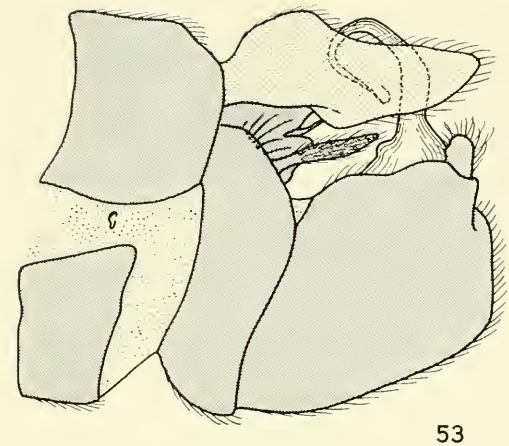
Bittacus walkeri Esben-Petersen 1915: 236-237 (no. fig.).

Type: ♂ holotype, South Africa (labelled "Dr. Smith, S. Afr. 44-6"); BMNH. The terminal abdominal segments have been removed, cleared, and mounted on a microscope slide. The specimen is otherwise intact except for minor damage to antennae, tarsi on right side, and one wing.

Range: Natal; March-April.

Walker (1853) had identified as *capensis* the specimen which later became the holotype of *B. walkeri*. Since the original description was not accompanied by illustrations, Esben-Petersen two years later (1917) redescribed *walkeri* and provided a photograph of the wings and a drawing of the terminal segments. Again, in 1921, he did the same, his drawing of the genitalia this time not as accurate as that published in 1917. Lestage (1929) only listed the species. Tjeder (1956) considered that a male from Krantz Kloof, Natal, identified as *walkeri* by Esben-Petersen (1917 ff.) and Wood (1933), was a new species, *angulosus* Tjeder. He described and illustrated both the male and female of *walkeri* and showed that three forms were involved in the complex that had been called *walkeri* (the third being *kimminsi* Tjeder, also from Natal).

Being slide-mounted, the terminalia of the holotype require some interpretation. Figure 53 shows the general outline. The conical projection from the lower edge of the epiandrial lobe seems to be glabrous and not densely sclerotized. Tjeder (1956) published a sketch by Kimmins showing the dorsal aspect of the epiandrial lobe. The concealed outlines of the aedeagus and proctiger can be made out because the specimen has been cleared (Figs. 53-54). There are no blackened spines on the inner surfaces of the epiandrium. The long, slender, dark-veined wings are characteristic (but see also *angulosus* and *kimminsi*); venation: Av present, Scv a short distance before FRs, two widely spaced Pcv.



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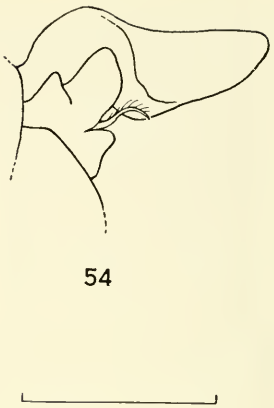

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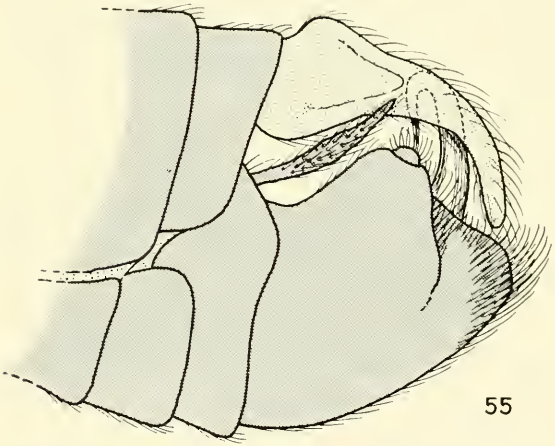

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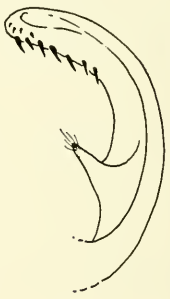

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FIGS. **53-54.** *Bittacus walkeri,* male holotype. **53,** terminal abdominal segments, left lateral aspect (mounted on microscope slide, therefore somewhat flattened); **54,** proctiger and right epiandrial lobe, left lateral aspect. FIGS. **55-56.** *Bittacus weelei,* male. **55,** terminal abdominal segments of lectotype, left lateral aspect; **56,** left epiandrial lobe of paralectotype from Katanga, dorsolateral aspect. Scale line 1 mm.

Bittacus weelei Esben-Petersen

Bittacus weelei Esben-Petersen 1913: 142-143, figs. 7 (♂ gen.), 8 (wing).
B. negus Navás 1915: 27.
B. longistigma Navás 1926a: 89, fig. 4 (wing). New synonymy.
B. wittei Navás 1933a: 315-316, fig. 93 (wing). New synonymy.

Types: 1 ♂, 1 ♀ syntypes, Kibonoto, cultivated zone, Kilimanjaro, 1905-1906, Sjöstedt; Stockholm. In the original description (1913), Esben-Petersen referred to these two specimens in the Stockholm Museum as "the type speci-

mens," although he also listed 1 ♂, 1 ♀ from Katanga, Congo, in the Tervuren Museum (which now also bear "Type" labels) and 1 ♀ from Congo in the Stockholm Museum, and remarked that he had "seen several specimens of this species." He did not comment on the whereabouts of an additional seven specimens in Sjöstedt's series of which the types were part (see Weele 1909, under *testaceus* Klug). Of the two syntypes in the Riksmuseet, Stockholm, I hereby designate as lectotype the male. It is labelled "Kilimandjaro, Sjöstedt. 1905-6"—"Kibonoto, kulturz., 7 April"—and "Type" (on a red tag), as well as having Weele's and Esben-Petersen's identification labels. The specimen is intact except for missing both front tarsi and part of the right hind tarsus.

Range: Tanzania, Uganda, southern Ethiopia, Democratic Republic of the Congo (Kasai, Katanga, Kivu), Malawi (Nyasaland), Rhodesia (Southern Rhodesia), and Cameroon; March-April, August, November-December. For a time, I regarded the Cameroon record (Lestage, 1929) with some doubt, but recently I have seen two males from Haute Volta (Saria, 12°16′N, 2°09′W, 9 July 1969; Paris Museum) that I consider to be *weelei,* although they are somewhat smaller than most individuals of the species. Smithers (1971) reports the species from three localities in Zambia, in December and January.

Esben-Petersen (1915) only listed *weelei;* in 1921, he redescribed it, illustrated the male genitalia, and placed *negus* Navás as a synonym of *weelei.* Lestage (1917) recorded *weelei* from Kindu, Congo, and compared it in a key with *testaceus.* In 1929, he too synonymized *negus* with *weelei,* suggested *longistigma* might also be a synonym, and recorded *weelei* from Cameroon, southern Ethiopia, Tanganyika, Uganda, Nyasaland and Belgian Congo. Navás (1929) listed *weelei* from Belgian Congo and Uganda, and in 1930 he recorded it from three Congolese localities, in November and December. Capra (1939) recorded it from Beni Sciangul (Beni Schangul, western Ethiopia, 10°52′N, 34°50′E), and noted the synonymy of *negus* (also from Ethiopia) with *weelei.* Smithers (1959) reported *weelei* from Southern Rhodesia (Zwipani, Urungwe Reserve, 17°00′S, 29°20′E, 12 and 17 December 1957) and included it in a key to Rhodesian bittacids.

When Navás first described *Bittacus negus* (1915), he noted the large size and elongate stigma. In 1922, he again described the species as new (same holotype), utilizing the same description and drawing attention to the elongate stigma as a diagnostic character. The illustration accompanying the second description omits vein 1A in the front wing. The holotype, in the Paris Museum, is from Boukrat, Ethiopia (coordinates unknown to me), 13 August 1904. The type is a female but now lacks the apical one-third of the abdomen, therefore can be effectively compared on the basis of wings only. It appears to me to agree well with *weelei.* This synonymy of *negus* with

weelei was stated by Esben-Petersen (1921), Lestage (1929) and Capra (1939).

Lestage (1929) strongly suggested the synonymy of *longistigma* Navás with *weelei,* although because he could base his argument only on venation and other wing characters he treated *longistigma* as a separate species. While the length of front wing in the holotype of *longistigma* is only 23.7 mm, this is within the range seen in specimens of *weelei.* Moreover, the number of cross-veins in the apical part of its wings is not sufficient to exclude it from *weelei,* which varies in this character. Accordingly, I agree with Lestage but venture to assert the synonymy. Navás thought that *longistigma* could be distinguished from all other African bittacids on the basis of the characteristic, elongate pterostigma (which is seen also, however, in *weelei*). He further stated that this character indicated the "closeness" of *longistigma* to *Klugius,* a genus he had erected for *Bittacus flavescens* of South America. (Perhaps it was because of his enthusiasm for this relationship that he used identical illustrations for the type of *longistigma* and for *"Klugius flavescens"* in separate papers both published in 1926.) The holotype is probably a male (apex of abdomen missing at time of description), labelled only "Deutsch. O. Afrika"; Deutsches Entomologisches Institut, Berlin-Friedrichshagen.

The holotype of *Bittacus wittei* was described by Navás as a female; however, the single specimen of this species in the collection in Tervuren—which bears all the correct label data and is designated "Type" and "*Bittacus wittei* ♀ Nav., det. Navás S. J."— is a male. Navás supposed *wittei* was near to but distinct from *B. walkeri.* Side-by-side comparison of the type of *wittei* with the male holotype of *B. weelei,* however, convinces me that both individuals represent the same species; and *weelei* is by 20 years the senior name for it. The type of *wittei* is from Lukafu, Katanga, Belgian Congo (10°31'S, 27°33'E), December 1930, G. F. de Witte.

I have illustrated the terminalia of the male lectotype of *weelei* in lateral aspect (Fig. 55) and an epiandrial lobe from the Katanga "syntype" (Fig. 56), rotated somewhat from dorsal aspect so as to show the sclerotized spines and conical projection on the mesal face. This is one of the largest species of *Bittacus,* some males having a front wing length of 30 mm. Its overall color is light reddish brown, the wings rather evenly but lightly tinged with grayish brown, the stigma long and somewhat elliptical. Venation: no Av, two widely spaced Pcv, Scv well beyond FRs (although Esben-Petersen, in 1921, described it as halfway between ORs and FRs).

Bittacus wittei Navás

See *B. weelei* Ebsen-Petersen.

Bittacus woodi Smithers

Bittacus woodi Smithers 1959: 180-183, figs. 1, 3 (♂ gen.), 2, 5 (♀ gen.), 4 (venation).

Types: ♂ holotype, Zwipani, Urungwe Reserve, Southern Rhodesia, 12 December 1957, R. Goodier; ♀ allotype, from light trap, Salisbury, Southern Rhodesia, December 1956; both in BMNH. Paratypes: 9 ♂, 5 ♀, Zwipani and Salisbury, various dates and repositories as listed by Smithers.

Range: Rhodesia (Zwipani is at 17°00′S, 29°20′E; Salisbury at 17°43′S, 31°03′E); late November to early February.

Smithers (1959) considered *montanus* as the only species likely to be confused with *woodi;* however, I consider *woodi* also very similar to *sobrinus* and less so to *selysi* and *peterseni.* This may be, as Smithers pointed out, the "variety" of *montanus* recorded by Kimmins (1957) from southeastern Katanga (Congo) and Northern Rhodesia (Zambia). Each epiandrial lobe has, near mid-length of the ventral margin, a more or less conical projection directed downward and mesad. The apex bears no teeth such as occur in *sobrinus.* Venation (after Smithers, 1959): Av present, Scv between ORs and FRs, two Pcv.

Bittacus zambezinus Navás

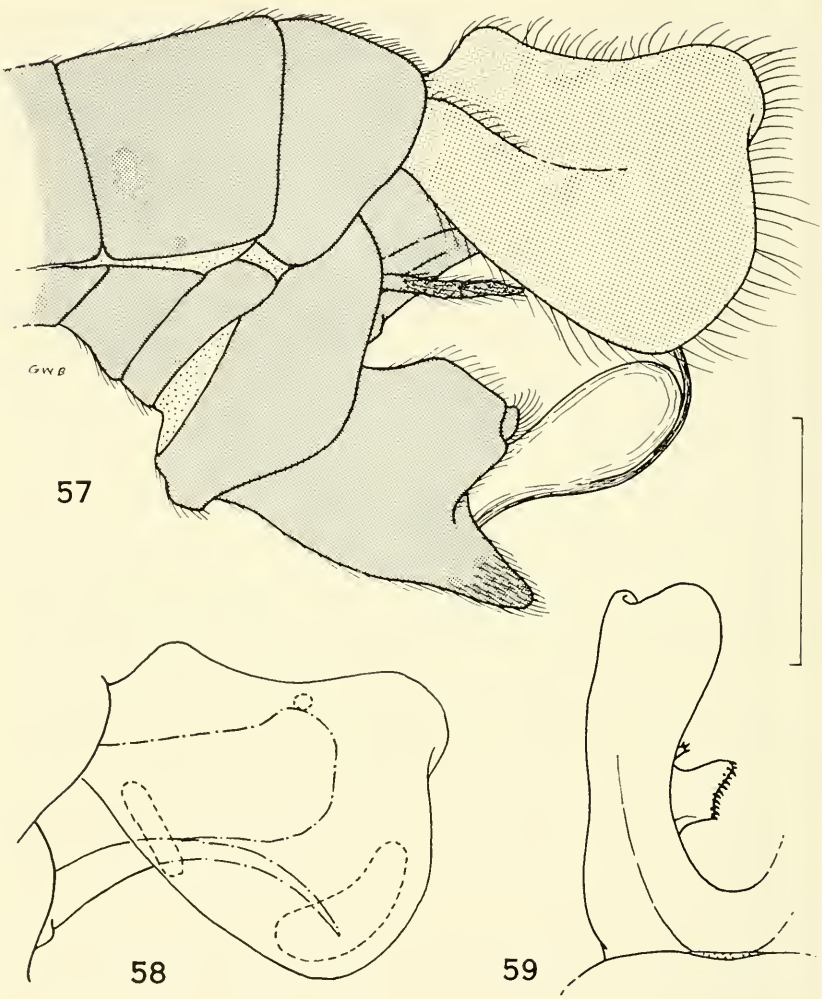
Bittacus zambezinus Navás 1931: 106-107, fig. 51 (♂ gen.).

Types: 2 ♂, 1 ♀ syntypes, labelled "Musèum Paris, Zambèze: Nova Choupanga près Chemba, P. Lesne," 9 March 1928; Paris (1 ♂, 1 ♀) and Barcelona (1 ♂). The male in the Paris Museum is hereby designated lectotype.

Range: Type locality only, on the Zambezi River, in central Mozambique. Coordinates of Chupanga are 18°02′S, 35°36′E; of Chemba, 17°09′S, 34°53′E; March.

Tjeder (1956) listed the species but had not seen specimens of it. He supposed the female was unknown; however, Navás gave measurements of the female.

Having broad epiandrial lobes, large penunci at the base of an elongate, filiform aedeagus, and a large, complicated proctiger, *Bittacus zambezinus* closely resembles *natalensis,* in South Africa, and has strong morphological similarities to *alluaudi* and *fumosus* from east-central Africa. My illustrations of the terminal abdominal segments (Figs. 57-59) were drawn from the male syntype in Barcelona; I later examined the types in the Paris Museum and found the male (lectotype) agreed in detail with these drawings. The fused basistyles are produced caudad as a subconical, hairy lobe beneath the base of the aedeagus (Fig. 57). Each epiandrial lobe has on its mesal face a small spine-tipped papilla near the upper margin, a broad spinose projection paralleling the lower basal margin, and an area of scattered short, black spines near the lower distal margin. The first two of these are visible in dorsal aspect (Fig. 59), and the positions of all are indicated by dashed lines in Figure 58. Also indicated in Figure 58, by dash-dot line, is the approximate



FIGS. **57-59.** *Bittacus zambezinus,* male lectotype. **57,** terminal abdominal segments, left lateral aspect; **58,** epiandrial lobe, lateral aspect, indicating outline of proctiger (dash-dot line) and spiniferous areas (dashed lines); **59,** right epiandrial lobe, dorsal aspect. Scale line 1 mm.

outline of the proctiger. Navás' description is fairly adequate for color characters but omits most of these useful structural details. Venation: no Av, two Pcv, and in each front wing two Scv, one before, one just beyond FRs, in the hind wings also two Scv, both before FRs.

This species differs from *natalensis,* as figured by Wood (1933, fig. 2), most obviously in the shape of the proctiger. As I am not certain that my interpretation of this structure, or Wood's, is free from error, I consider the

relationship of these two forms a problem that ought to be further investigated.

Bittacus zavattarii Capra

See *B. alluaudi* Navás

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